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Effects of Fire and Rehabilitation Seeding on Sage Grouse Habitat in the Pinyon-Juniper Zone

Final Report

Effects of Fire and Rehabilitation Seeding on Sage Grouse Habitat in the Pinyon–Juniper Zone

(JFSP 01B-3-3-01)

Joint Venture Agreement 01-JV-11222074-102 (Stanford SPO reference #2024114) between the USDA Forest Service, Rocky Mountain Research Station, and Stanford University

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Stanford University has been a cooperator in the Joint Fire Sciences project "Effects of Fire and Rehabilitation Seeding on Sage Grouse Habitat in the Pinyon–Juniper Zone" (JFSP 01B-3-3-01).

Major objectives of the project were to examine the effects of fire and seeding within pinyon-juniper dominated ecosystems on (1) site stability and recovery potential of sagebrush communities, (2) nutritional properties and establishment characteristics of plant species required by sage grouse, and (3) occurrence and abundance of sage grouse and other sagebrush-obligate birds. Under Joint Venture Agreement 01-JV-11222074-102, Stanford University was responsible for examining the potential effects of prescribed fire on distributional patterns of birds and vegetation that serves as bird habitats.

As Stanford's Technical Representative, I collaborated with the Forest Service to prepare a mutually acceptable work plan, developed an appropriate methodology, and completed four years of data collection on birds and their habitats. Work supported by the Joint Fire Sciences Program proved highly complementary to our ongoing efforts to understand patterns of faunal diversity in the central Great Basin, the potential mechanisms underlying those patterns, and inferences for management that can be drawn from such knowledge. Research supported by the second phase of Joint Venture Agreement 01-JV-11222074-102 (JFSP 01B-3-3-01) led to the preparation and submission of 17 manuscripts in peer-reviewed journals (13 published or in press, four in review), a book chapter, two M.S. theses, seven invited presentations, and three contributed presentations.

In this final report, I summarize some of our most recent research results. Work on alternative predictors of species richness and number of rare species is in review with *Journal of Biogeography*. Work on patterns of spatial autocorrelation of assemblages of birds, vegetation composition, vegetation structure, and productivity is in review with *Diversity and Distributions*. I also attach copies of three recent peer-reviewed publications.

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PRODUCTS SUPPORTED BY "EFFECTS OF FIRE AND REHABILITATION SEEDING ON SAGE GROUSE HABITAT IN THE PINYON-JUNIPER ZONE," JFSP 01B-3-3-01

Peer-reviewed publications

Fleishman, E., C.J. Betrus, R.B. Blair, R. Mac Nally, and D.D. Murphy. 2002. Nestedness analysis and conservation planning: the importance of place, environment, and life history across taxonomic groups. Oecologia 133:78–89.

Fleishman, E., C.J. Betrus, and R.B. Blair. 2003. Effects of spatial scale and taxonomic group on partitioning of butterfly and bird diversity in the Great Basin. Landscape Ecology 18:675–685.

Fleishman, E., C.J. Betrus, and L.P. Bulluck. 2003. Annual variability of species richness and composition of breeding birds in the central Great Basin. Great Basin Birds 6(1):36–44.

Bailey, S-A., S. Anderson, K. Carney, E. Cleland, M.C. Horner-Devine, G. Luck, L.A. Moore, C. Betrus, and E. Fleishman. 2004. Primary productivity and species richness: relationships among functional guilds, residency groups and vagility classes at multiple spatial scales. Ecography 27:207–217.

Fleishman, E., J.B. Dunham, P.F. Brussard, and D.D. Murphy. 2004. Explanation, prediction, and maintenance of native species richness and composition in the central Great Basin. Pages 232–260 in J.C. Chambers and J.R. Miller, editors. Great Basin riparian ecosystems—ecology, management, and restoration. Island Press, Washington, D.C.

Fleishman, E. and R. Mac Nally. 2002–2003 (2004). Linking models of species occurrence and landscape reconstruction. Transactions of the Western Section of the Wildlife Society 38/39:1–4.

Mac Nally, R., E. Fleishman, L. Bulluck, and C. Betrus. 2004. Comparative influence of spatial scale on beta diversity within regional assemblages of birds and butterflies. Journal of Biogeography 31:917–929.

Seto, K.C., E. Fleishman, J.P. Fay, and C.J. Betrus. 2004. Linking spatial patterns of butterfly and bird species richness with Landsat TM derived NDVI. International Journal of Remote Sensing 25:4309–4324.

Betrus, C.J., E. Fleishman, and R.B. Blair. 2005. Cross-taxonomic potential and spatial transferability of an umbrella species index. Journal of Environmental Management 74:79–87.

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Fleishman, E., J.R. Thomson, R. Mac Nally, D.D. Murphy, and J.P. Fay. 2005. Predicting species richness of multiple taxonomic groups using indicator species and genetic algorithms. Conservation Biology 19:1125–1137.

Thomson, J.R., E. Fleishman, R. Mac Nally, and D.S. Dobkin. 2005. Influence of the temporal resolution of data on the success of indicator species models of species richness across multiple taxonomic groups. Biological Conservation 124:503–518.

Bulluck, L.P., E. Fleishman, C.J. Betrus, and R.B. Blair. In press. Spatial and temporal variation in species occurrence rate affects the accuracy of occurrence models. Global Ecology and Biogeography.

Fleishman, E., R. Mac Nally, and J.R. Thomson. In press. Challenges and opportunities for conserving faunal biodiversity in arid ecosystems. Invited paper. Annals of Arid Zone.

Manuscripts in review

Drake, J.M., E.E. Cleland, C. Bowles, K. Carney, M.C. Horner-Devine, S. Emery, J. Gramling, M.D. Smith, D.B. Vandermast, E. Fleishman, and J.B. Grace. Do non-native plant species affect the shape of productivity-diversity relationships? Evaluating the curvature hypothesis in six North American ecosystems. Functional Ecology.

Fleishman, E., R. Donnelly, and J.P. Fay. Applications of nestedness analyses to biodiversity conservation in developing landscapes. Landscape and Urban Planning.

Fleishman, E. and R. Mac Nally. Patterns of spatial autocorrelation of assemblages of birds, floristics, physiognomy, and productivity in the central Great Basin, USA. Diversity and Distributions.

Thomson, J.R., E. Fleishman, R. Mac Nally, and D.S. Dobkin. Comparison of predictor sets for species richness and the number of rare species of butterflies and birds. Journal of Biogeography.

Master of Science theses

Betrus, C. J. 2002. Refining the umbrella index complex: an application to bird and butterfly communities in montane canyons in the Great Basin. M.S. thesis, Miami University, Oxford, Ohio.

Penfield, L. 2003. An exploration of accuracy issues regarding predictive models of avian occurrence in the central Great Basin. M.S. thesis, Miami University, Oxford, Ohio.

Invited presentations

2004. Fleishman, E. and R.B. Blair. The importance of place, environment, and life history across taxonomic groups for conservation planning in urbanizing environments. Ecological Society of America, Portland, Oregon.

2004. Signal, noise, and taxonomic effects in biodiversity patterns. The Wildlife Society, Calgary, Alberta.

2004. Surrogate-based approaches for predicting species richness of multiple taxonomic groups. North Dakota State University.

2004. Surrogate-based approaches for predicting species richness of multiple taxonomic groups. University of North Dakota.

2005. Surrogate-based approaches for predicting species richness of multiple taxonomic groups. Bowling Green State University.

2005. Fleishman, E. and D. Dobkin. Predictive modeling of the distribution and habitat of birds in managed landscapes. USGS Forest and Rangeland Ecosystem Science Center, Snake River Field Station, Boise, Idaho.

2005. Tradeoffs among alternative predictors of species distributions. Predictive modelling of species distributions: new tools for the 21st century. Universidad Internacional de Andalucía, Spain.

Contributed presentations

2003. Blair, R.B. and E. Fleishman. Selecting effective umbrella species for protection and management: the umbrella species index. Natural Areas Conference, Madison, Wisconsin.

2004. Thomson, J.R., R. Mac Nally, and E. Fleishman. "Evolving" distributional models for birds and butterflies. Ecological Society of Australia, Adelaide.

2005. Fleishman, E., J.R. Thomson, and R. Mac Nally. Surrogate-based approaches for predicting species richness of multiple taxonomic groups. Society for Conservation Biology, Brasília, Brazil.

INTRODUCTION

From 2001–2005, with support from the Joint Fire Sciences Program, we collected data on the distribution and abundance of breeding birds from a total of 298 points in the Shoshone, Toiyabe, and Toquima ranges (Humboldt–Toiyabe National Forest). At those points, we also collected data on vegetation structure, plant composition, and other attributes of bird habitat. Most of the points were located in pinyon-juniper or riparian woodland. Fourteen points were located in the Demonstration Watershed and 10 were located in an adjacent control watershed. Eleven points (six "treated," five control) were established in Wall Canyon (Toiyabe Range), in which a wildfire occurred in high-density pinyon-juniper woodland in 2000.

The total area treated with prescribed fire in the Demonstration Watershed prior to 2004 (~20 ha) was insufficient to assess reliably the response of birds and their habitats to watershed-scale burns. Multiple-year surveys in the Watershed and beyond, however, afforded us a valuable opportunity to examine deterministic and stochastic influences on species richness and composition of birds. In addition, surveys provided insights to monitoring approaches likely to provide reliable information about biological responses to an array of environmental changes, including but not limited to fuels management.

METHODS

Data for birds were collected using established techniques that detect species presence reliably. Each year, we sampled birds during the breeding season (late May through June) using 75-m variable-radius point counts, an effective method for riparian areas and uplands in the Great Basin. Before selecting sampling points, we divided each of our study canyons into multiple segments from base to crest. Each segment was long enough to span a 100-m change in elevation. Within a segment, points were located in each of the dominant vegetation types (usually two or three points per segment). Most points were established > 200 m apart (i.e., 350 m between point centers); territory sizes of birds during the breeding season typically are smaller than distances between neighboring sampling points. Point counts were conducted only in calm weather, and none were conducted > 3.5 hours after dawn. Each point was visited three times per year. We measured geographic coordinates at the center of the point with a GPS.

To characterize vegetation structure and composition, we established three vegetation sampling plots at each bird point. We measured three radial 30-m lines, separated by 120°, from the center of the point count location. The end of each line served as the center of a circular vegetation sampling plot with 11.3 m radius (0.04 ha). Each plot was divided into four quadrants. Within each quadrant, we recorded the size of all live trees (either diameter at breast height [dbh] or basal diameter, depending on plant morphology) and the identity of all live trees. Trees generally were defined as woody vegetation > 1 m in height and ≥ 5 cm dbh. We also recorded the size and, where possible, the identity of standing or fallen dead trees.

We used a concave spherical densiometer to estimate proportion of canopy cover. To estimate cover of shrubs, ground vegetation, litter, and bare ground, we used an ocular tube. Ocular tube measurements were taken at a 45° angle downward from the line of sight. When vegetation was present, we recorded the occurrence of dominant species (approximately 25 different taxa; most grasses and forbs were not treated separately). We collected 21 densiometer and ocular tube readings at each bird point: one each at 8 m, 16 m, and 24 m along the 30 m line from the center of the bird point to the perimeter of each circular vegetation plot; and one while facing in each of the four cardinal directions from the center of each circular plot. Cover values for each structural layer (canopy, shrubs, ground vegetation, and bare ground) were averaged at each bird point. Occurrence data for individual species or taxonomic groups of plants were aggregated into a relative measure of cover at each bird point. Taxa detected in very few points were not included in our analyses.

To estimate primary productivity in a 30 m x 30 m pixel at the center of each point, we calculated the normalized difference vegetation index (NDVI), a measure of "greenness" that is an extensively used vegetation ratio in remote sensing. We derived NDVI measures from a single cloud-free, geo-corrected Landsat 7 EMT+ image (WRS 41 / 33) acquired in June 2002, coincident with the peak growing season and the most active period for breeding birds in the Great Basin. Examination of satellite images from the late 1970s to present indicates that within our study system, NDVI in a given location is not highly variable over time and that spatial patterns of NDVI are relatively consistent over time.

Sites were delineated by overlaying differentially corrected global positioning system locations on a 30-m (1:24,000) digital elevation model maintained on a GIS. Geographic coordinates and 14 uncorrelated ($R_{Pearson} < 0.6$) topographic and topoclimatic variables were measured for each site. Most were derived from electronic sources of data in combination with ArcView and Arc Macro Language scripts. All of the variables reasonably could be expected, a priori, to have functional relationships with distribution patterns of birds.

COMPARISON OF PREDICTOR SETS FOR SPECIES RICHNESS AND THE NUMBER OF RARE SPECIES OF BIRDS

Protection of locations with high native species richness generally is thought to be an efficient way to conserve overall biological diversity and to sustain key ecological functions. Moreover, species richness has been measured in many places over long periods of time and typically is more practical to assess and to monitor than abundance or demographic variables. Conservation planning sometimes weights measures of species richness by rarity, which often has been equated with small geographic range, low abundance, or both. Although total number of species and number of rare species frequently are correlated, rarity can be driven by a complex array of mechanisms, and rare species often do not occur in the same locations or in locations with highest species richness. Therefore, effective methods to measure and manage rare species may differ from those directed toward species richness.

Any number of environmental variables may be associated with the distribution of species richness and the number of rare species and used as predictor variables for modeling. Inevitably, there is a trade-off between the quality of information provided by predictor variables and the cost of obtaining that information. Collection of field data on vegetation composition and structure generally does not require extensive, specialized training and many established protocols are available. Data gathering may be time-consuming, however, and fine-grained information on vegetation composition and structure remains difficult to characterize well using remote sensing. With geographic information systems (GIS) and appropriate software, measures of topography or topoclimate can be derived at low cost from existing electronic sources of data such as digital elevation models. Variables also can be estimated for locations that have not been visited. Remotely sensed data for variables associated with photosynthetically active biomass and net primary productivity have similar advantages.

Workers also have built functional relationships between species richness and the occurrence of "indicator" species, defined here as a small set of species with occurrence patterns that functionally are related to species richness of a larger set of organisms. If validation data sets demonstrate that the functional models make accurate predictions, then—depending on the target system and the level of expertise of the individuals conducting surveys—it may be far more feasible to measure occurrence of a small number of indicator species than to conduct comprehensive species inventories.

We compared the effectiveness of three different types of predictor variables, indicator species, vegetation, and topoclimate, as predictors of the total number of species (species richness) and the number of rare species of birds.

We used Poisson regression with Bayesian model averaging to predict species richness and the number of rare species. Poisson regression is a generalized linear model with a logarithmic link function and an assumed Poisson distribution for the response variable. Bayesian model averaging incorporates uncertainty in model-selection into statistical inference and prediction and consistently has been shown to produce more accurate predictions than methods that select a single best model. We compared expected prediction success of all models using both internal validation trials (bootstrapping) and external validation trials. We performed the external validation using data from 25 sites in the Toiyabe Range that have similar environmental profiles to sites used in model building and bootstrapping. The validation sites were surveyed in 2004, after the model building data were compiled. We assessed predictive performance primarily on the basis of Spearman rank correlations between predicted and observed species richness because the ability to rank sites by relative species richness or number of rare species generally will be more relevant to conservation planning than predicting the exact number of species or rare species in each site.

Internal validation demonstrated that bird indicator species were the most successful predictors of the rank order of sites with respect to species richness of birds and the number of rare bird species. Predictions of bird species richness based on bird indicator species were good (R_S = 0.81), but predictions of the number of rare bird species were poor (R_S = 0.45). Butterfly indicator species were reasonable predictors of species richness of birds (R_S = 0.68) and were more accurate predictors than vegetation variables (R_S = 0.56), topoclimate variables (R_S = 0.61) or a combination of vegetation and topoclimate variables (R_S = 0.57). Topoclimate variables were better predictors of the number of rare bird species than vegetation variables, all environmental variables, or butterfly indicator species, but all sets of predictions were poor (R_S < 0.50). In general, predictions of species richness of birds and the number of rare bird species were not improved by combining either vegetation variables or topoclimate variables with data for bird indicator species or butterfly indicator species.

External validations confirmed that bird indicator species were the most accurate predictors of species richness of birds ($R_s = 0.84$). Butterfly indicator species and topoclimate variables performed worse than expected on the basis of bootstrapping results and produced poorer predictions than vegetation variables. Different sets of indicator species had the strongest functional relationships with species richness and with number of rare species. In general, the ability to predict numbers of rare species based on any set of candidate predictors was weaker than the ability to predict species richness, which may result from the high degree of stochasticity that often characterizes distributions of rare species.

Predictions based on vegetation variables, either alone or in combination with other types of candidate predictors, often were the least accurate. These inaccuracies resulted from substantial variability in vegetation among sites. If model-testing sites have values that fall outside the range of values included in the model-building data, predictions for those test sites often will be inaccurate. The difficulty of making predictions for new sites with environmental characteristics that are different from environmental characteristics at sites for which species data exist highlights a potential disadvantage of using vegetation variables as predictors in regions with heterogeneous land cover.

Two considerations are fundamental to conservation practice: information content and cost efficiency. A predictive model may be extremely reliable, but its applicability will be limited unless measurement of the predictors is relatively fast and easy. Our results highlight the difficulty in identifying dependable predictors of the distribution of rare species. Successful occurrence models have been developed for one rare species (although they may not be more efficient than conducting surveys directly for the target species), but it remains difficult to predict the number of rare species in a given location. Even when predictors that are "good enough" can be identified, those predictors are likely to be different from the set selected as predictors of species richness of the same taxonomic group.

Field measurements of habitat; measures of topography, climate, and land cover derived from GIS and remote sensing; and the occurrence patterns of small sets of "indicator" species frequently are considered as surrogate measures of faunal distributional patterns. Of these, measures derived from GIS and remote sensing are the fastest, easiest, and cheapest to calculate. Whether predictions of species richness and number of rare species based on topoclimate variables in our study system would be sufficiently reliable depends on the context in which information is used. Land-use decisions that are relatively difficult to reverse (e.g. authorization of a new mine) may demand a higher level of accuracy than situations in which land use can be modified or reversed through an iterative management process (e.g. adjusting the number of livestock permitted to graze in a given location).

In our study system, indicator species were the most accurate tools for predicting species richness and number of rare species. Our statistical methods select indicator species potentially applicable across extensive areas on the basis of data that are collected from a small fraction of the total land area. For some geographic areas and taxonomic groups, observers can save time and money by searching for a subset of an assemblage rather than trying to survey all species in the assemblage. In these situations, validated predictive models based on indicator species may be a realistic method for deriving data on distribution patterns that can inform land-use planning.

PATTERNS OF SPATIAL AUTOCORRELATION OF ASSEMBLAGES OF BIRDS, VEGETATION COMPOSITION AND STRUCTURE, AND PRODUCTIVITY

Spatial structure often is treated as a nuisance that must be accounted for to improve the statistical properties of tests. Nevertheless, spatial structure potentially offers many insights into ecological patterns and processes. Because many distributional patterns are not spatially independent, it is useful to identify the lag (difference in space) over which a pattern is autocorrelated and to characterize the functional form of the autocorrelation. If a response variable and a potential predictor variable have similar patterns of autocorrelation, it may be reasonable to infer either a causal relationship or that both variables are responding similarly to another phenomenon.

Many studies have addressed spatial autocorrelation in species richness, abundance, or assemblage composition of birds. Especially at relatively large spatial extents, measurements associated with potential mechanisms often have been derived from GIS and remote sensing. Here, we focus on spatial autocorrelation of avian composition and three aspects of birds' habitats: floristics (taxonomic composition of the vegetation), physiognomy (physical structure of the vegetation), and the normalized difference vegetation index (NDVI), a measure of "greenness" that serves as an estimate of primary productivity.

Geostatistical analyses usually model spatial autocorrelation with semivariograms, which are representations of variances in a variable (e.g. mineral concentration) as a function of distance (also called spatial lag). Different semivariogram models characterize different types of spatial phenomena. In many cases, prior knowledge about the model most likely to fit a given phenomenon does not exist, or there may be valid alternative hypotheses. We fitted a set of the most commonly used semivariogram models to measures of the similarity of bird assemblages, floristics, vegetation structure, and estimated productivity at 140 sites in the mountains of the central Great Basin (Lander and Nye counties, Nevada, USA). The primary objective of our work was to examine whether the pattern of spatial autocorrelation for birds was concordant with, and hence might in part be explained by, patterns of spatial autocorrelation of floristics, vegetation structure, and estimated productivity.

We used data on geographic coordinates, abundances of 79 species of birds, floristics, vegetation structure, and NDVI at 140 sampling points to build a matrix of dissimilarities for each response variable. This process generated geographic separations (linear distances) and dissimilarity values for each response variable at 9730 pairs of points. We used the Canberra distance as our measure of dissimilarity for bird assemblages, floristics, and vegetation structure. Our measure of dissimilarity for NDVI was mean difference.

For each of the four response variables, we calculated eight of the most commonly used (isotropic) semivariogram models: (1) linear, (2) spherical, (3) exponential, (4) Gaussian, (5) wave (or sine-hole), (6) cubic, (7) Matérn ($\gamma = 3/2$), and (8) power-law. Different semivariogram models characterize different types of spatial phenomena. For example, many spatially autocorrelated phenomena follow a spherical model—spatial autocorrelation decreases linearly to a certain lag and reaches an asymptote, beyond which the locations are statistically uncorrelated and can be regarded as "independent." Exponential models are similar to spherical models, but the spatial autocorrelation approaches its maximum value asymptotically.

Three parameters describe most semivariogram models. The first parameter, the range, is the geographic separation at which semivariogram values become constant (i.e. the distance at which the response variable no longer is spatially autocorrelated). The second parameter, the nugget, is the estimated dissimilarity as the geographic separation approaches zero. The third parameter, the sill, is the dissimilarity value at the range. Linear and power-law models have nugget parameters but neither has a range or a sill; both have a slope parameter. The power-law model also has an exponent parameter.

We used Bayesian model-fitting to compute semivariograms. We first grouped values for each response variable into bins with lag distances of 1 km. For each bin, we computed the mean dissimilarity (γ_d) and the variance of the dissimilarity (V_d = 1/precision). We grouped all site-pairs with geographic separations > 62 km into one bin because sample sizes (N_d) were relatively low for km-wide bins at those lags. We used the Bayesian Information Criterion to identify the best semivariogram model for each of the four response variables. Criterion-based approaches seek the smallest value (i.e. most negative BIC) for the criterion because the goal is to minimize a function of a weighted sum of model fit and model complexity. Models with BIC values that differ by less than three are held to have similar statistical support.

The best fit for avifaunal composition was a spherical model. Fits for cubic and exponential semivariogram models were within three BIC units of the fit of the spherical model. Based on the parameters for the spherical model, avifaunal composition was spatially autocorrelated at lag distances from 0–29.6 km; mean Canberra dissimilarities increased rapidly from a mean of 0.38 for lag distances of 0–1 km to 0.53 at the range.

Floristics data were spatially autocorrelated at lag distances from 0–20.1 km. A spherical semivariogram model was the best fit to the data. Modeled dissimilarity values increased from 0.40 at lag distances 0–1 km to an asymptotic value of 0.53. The dissimilarity curve was relatively smooth up to the sill. The best-fitting semivariogram model for vegetation structure was the power-law. Although the semivariogram did not attain an asymptote (by definition), the semivariogram was relatively flat, suggesting that vegetation structure was fairly homogenous regardless of lag distance. NDVI was spatially autocorrelated at lag distances from 0–58.1 km, with a nugget of 0.08 and a sill of 0.13. A spherical model was the best fit to the NDVI data.

In summary, we found that species composition of birds was spatially autocorrelated over a larger lag distance than floristics, but over a much smaller distance than NDVI or vegetation structure, which did not attain an asymptote over the range of measured lag distances.

Dissimilarity values for birds were relatively high at all distances measured. This is consistent with previous work in our study system that found considerable spatial variation in species composition of birds, averaged across all lag distances, regardless of sampling resolution. The range value for birds (ca 30 km) was lower than the greatest lag distance for points within a mountain range (ca 35 km). There is substantial evidence that individual mountain ranges function as permeable but distinct islands of habitat for many taxa whose resources in the arid valleys separating the mountain ranges are scarce. In addition, although the mountain ranges we surveyed are in the same ecological province, differences in elevation and precipitation at the mountain range level lead to some differences in land cover.

Species composition of birds and floristics both were described best by a spherical model. Dissimilarity values for avifaunal composition were slightly lower than values for floristics at very small lag distances, but were similar at the asymptotic maximum. These results suggest that the spatial pattern of avifaunal composition in the montane central Great Basin is influenced more strongly by floristics than by vegetation structure. This does not imply that the structure of vegetation plays no role in where different species of birds occur, but spatial dissimilarities in species composition were not concordant with our measures of vegetation structure. It is possible that one or more variables associated with vegetation structure (e.g. canopy cover or number of live trees) would be more closely associated with avifaunal composition than our aggregate assessment of vegetation structure.

It is possible that species composition of birds and species composition of plants have similar responses to abiotic environmental gradients. These relationships may be fairly common in desert ecosystems across southwestern North America where availability of water is a primary driver of biodiversity patterns and ecological processes. Lack of correspondence between spatial patterns of bird composition and vegetation structure also may suggest that avifaunal assembly in our study system is influenced by population dynamics or dispersal history. Many of the species we recorded are not residents; they breed but do not winter in the study system. If availability of nesting sites is not strongly limited, individuals may select territories from a suite of potentially suitable locations. On the basis of which territories are occupied in a given year, there may be substantial variation in the attributes that are inferred to be important in birds' use of habitats. A not mutually exclusive explanation is that some birds may select territories on the basis of "greenness" rather than a certain vegetational profile. The differences in models for the three vegetation variables suggest that estimated productivity in this system cannot be predicted as a simple function of floristics and vegetation structure.

Distributions of birds may be affected more by the presence or quantity of different resources in the landscape than by the structural arrangement of those habitat types. Indeed, the difference between autocorrelation ranges for birds and floristics probably reflects differences in dispersal ability between birds and plants. As the lag distance over which spatial autocorrelation is present decreases, it implies that spatial variation increasingly is structured in patches. This suggests that in our study system, the distributions of plant species are more patchy than the distributions of birds.

Spatial autocorrelation often is seen in a negative light by ecologists because it reduces statistical independence. Explicitly accounting for spatial autocorrelation, however, increases the reliability of inferences about relationships between distributional patterns and potential predictor variables. Spatial autocorrelation modeling has considerable potential to derive insights about the potential causes of distributional patterns of focal taxa and to help ensure that ecological processes supporting biodiversity patterns are managed appropriately.

LINKING MODELS OF SPECIES OCCURRENCE AND LANDSCAPE RECONSTRUCTION

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Ecologists and land managers around the world are charged with first arresting and then reversing declines in native species. Revegetation has been proposed as one of the mechanisms by which landscapes can be rehabilitated to support viable populations of native wildlife. Because large-scale revegetation often proves to be technically difficult and costly, it is critical to evaluate the likely outcome of alternative proposals for landscape reconstruction. Here we describe a new approach for examining the potential effects of spatially extensive ecological restoration on species of concern. Our method links validated models of species occurrence with GIS-based models of various revegetation scenarios to estimate the range of biodiversity responses under each option.

Explaining and predicting species occurrence long has been a major goal in ecology, conservation biology, and wildlife management (Rosenzweig 1995, Mac Nally 1995, Bell 2001). There are many possible ways to predict species occurrence. Traditional 'habitat modeling'-predicting occurrence as a function of resource requirements, such as food sources or nesting sites-may have a high probability of success (Hanski 1999, Miller and Cale 2000), but obtaining such data can be expensive, particularly over extensive areas. Therefore, predicting species occurrence as a function of environmental variables that can be quantified easily, at small spatial grains, and over large areas, is appealing (Austin et al. 1990, Guisan and Zimmerman 2000, Jackson et al. 2000).

We recently developed a statistically rigorous framework for examining the generality of predictors of species occurrence using an iterative process of model building, testing, and refinement (Fleishman et al. 2001, in press). We make extensive use of Bayes-based methods, which facilitate more detailed and practical assessment and improvement of predictions than conventional approaches (Ellison 1996, Sit and Taylor 1998). Our framework seeks to identify predictors of species occurrence at grain sizes on the order of several km^2 over extents of 100s to 1000s of km^2. This corresponds to the scale at which many land-use decisions must be made.

To be useful, the predictions of species-occurrence models must be tested using explicit standards (Guisan and Zimmerman 2000, Jackson et al. 2000). We test our models-which effectively are hypotheses about predictors of species distributions-using independent data that were not used to build the models (Fleishman et al. in press). The process of generating and testing model predictions increases our understanding of relationships between organisms and environmental variables and contributes to the scientific foundation for regional conservation and management (Mac Nally and Bennett 1997, Hawkins et al. 2000, Mac Nally et al. 2000).

Species-specific occurrence modeling has been employed widely in the past (Braithwaite et al. 1989, Lindenmayer et al. 1990, Scott et al. 2002), but occurrence models rarely have been linked with GIS-based models of alternative management strategies or revegetated landscapes (Bennett 1999, Marzluff et al. 2002). The alternatives we develop are based on ecological vegetation classes, which are defined as one or more similar floristic communities that exist under a common regime of ecological processes and that are linked to broad landscape features (Muir et al. 1995). Because ecological vegetation classes are closely connected with broad-scale topographic, edaphic, and climatic variables, they are a useful link between vegetation and landscape-scale planning and management. Alternatives vary with respect to the amount and spatial configuration of different ecological vegetation classes. Our approach recognizes that not only is there a spectrum of habitat quality (McIntyre and Barrett 1992), but also that animals respond to more than one vegetational community (Mac Nally et al. 2002).

Connecting occurrence models with revegetation models allows us to estimate the quantity and distribution of suitable habitat for each species that would be available under each scenario. By treating models for individual species as probabilistic, we can generate ranges of outcomes (i.e., confidence intervals) for each alternative. Thus, we can gauge the overall potential of each alternative to achieve specified ecological objectives.

MODELING FRAMEWORK

Our modeling approach involves 4 main steps. We have successfully applied the first 2 steps to a study system in North America. We currently are laying the biological and collaborative groundwork to apply all 4 steps to a second study system in Australia. First, we develop species-specific occurrence models (Fleishman et al. 2001). We derive potential predictors of species occurrence, such as elevation, topographic heterogeneity, and precipitation, from GIS-based models of topography and climate. We have devised a process to exhaustively search through millions of possible models for each species of animal (there are 2^Q models for Q predictor variables). After reducing the set of predictors to a relatively small number of variables (usually ≤ 6), we fit models using Bayesian logistic methods. Bayesian approaches are useful because they generate distributions (rather than point estimates) for the probability that a species will be present in a given location.

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Second, we validate the models by conducting new, independent field surveys of species occurrence at locations that were not used to build the models (Fleishman et al. in press). The Bayesian model for each species, with computed regression-coefficient distributions, is used with data for the predictor variables from the new locations to generate probability distributions for occurrences at those new locations. The reliability of species-specific models is assessed by compiling the numbers of successful predictions. This phase also identifies those species whose distributions are either inherently difficult to predict or for which model predictions are poorer than expected. In many cases, validation data can be used to improve models (i.e., to alter values of model parameters or to remove or include different independent variables). Third, we use GIS to specify alternative reconstruction scenarios-to emulate alternative distributions of ecological vegetation classes across the landscape. This approach is applicable to virtually any landscape, and scenarios can be based on any combination of ecological, land management, or economic criteria. For example, we can simulate how the percent cover of native vegetation in the landscape might be increased to a target threshold by replanting (1) different amounts of the most depleted ecological vegetation classes, (2) locations least able to support economic uses such as agriculture, (3) locations that have been subject to the most severe human impacts, or (4) ecological vegetation classes that are least expensive and most biologically feasible to restore. In practice, creation of explicit scenarios will depend on the physical and biological attributes of the planning area and the priorities and constraints of the relevant public or private land managers.

Finally, we link the alternative reconstruction scenarios with the species-specific models to evaluate the potential effectiveness of each scenario in sustaining or increasing native biodiversity. Again using GIS, we compute species-specific logistic models corresponding to each alternative reconstruction scenario. This step provides probability fields of occurrence across the landscape based on the pertinent environmental variables. For each species, we estimate the total area that would be "highly likely" (say, $\geq 70\%$ probability) to support the species according to each reconstruction scenario. After the species-specific results have been computed, we can estimate the biological success of alternative scenarios using a variety of criteria. For example, we might simply calculate total area with a high probability of supporting occupancy. We also might differentially weight taxa by conservation concern-e.g., high weightings for threatened species, no weighting for ubiquitous species.

CASE STUDIES

We focused on butterflies in the Great Basin of western North America as our initial study system. In temperate ecoregions, butterflies are well understood ecologically, easy to study and monitor, and may respond rapidly to management (New 1991, Holl 1995, Blair and Launer 1997). Biological research in the Great Basin has yielded landmark contributions to ecology and biogeography (e.g., Brown 1971, Lomolino 1996). The Great Basin also is an appropriate focal system from a natural resource perspective, as more than 75% of the ecoregion is public land that is managed under multiple-use mandates.

We used 14 topographically based, GIS derived environmental variables (and, to capture possible non-linear responses, their squares) from 49 locations in the Toquima Range (Lander and Nye Counties, Nevada, USA) and species inventories conducted over 4 years (1996-1999) to model logistically occurrence of resident butterfly species in the Great Basin. We obtained statistically significant models for 36 of the 56 species (Fleishman et al. 2001). To test the models, we collected new validation data from 39 locations in the nearby (ca 40 km) and ecologically similar Shoshone Mountains. We conducted inventories of butterflies in 22 locations in 2000-2001 and in another 17 locations in 2001.

Validation tests (Fleishman et al. in press) showed that success rates for predicted absences were uniformly higher than for predicted presences. Increasing the temporal extent of data from 1 to 2 years elevated success rates for predicted presences but decreased success rates for predicted absences, leaving the overall success rates essentially the same. Model fit (measured by the explained deviance) was an indicator of the probable success rate of predicted presences. Occurrence rates for several species differed dramatically between the model-building and model-validation data sets, suggesting that some of the locations used to build models should be inventoried again during the validation phase to discriminate between temporal and spatial sources of variability in occupancy. To refine the models, we will use existing and new validation data to 'update' model parameter estimates to improve the fit and/or predictive success of models for species that were not modeled well in the first iteration.

Our work in the Great Basin serves as a template for conducting parallel exercises with other taxonomic groups or in different study areas. We have initiated comparable assessments of birds and mammals in the box-ironbark forests of central Victoria, Australia, in which 85% of presettlement vegetation has been lost (Environment Conservation Council 2000). Managers in the 2 ecoregions confront similar patterns of landscape degradation and its impacts on native wildlife. However, the study areas have different management and legislative infrastructures, biotas, and evolutionary histories. These correspondences and contrasts allow us to evaluate the generality of our approach and, therefore, the practical applicability of its outcomes.

In the box-ironbark forests, we have surveyed birds in 160 locations in a 30,000 km^2 region over 2 full years (Mac Nally et al. 2000, 2002). 80 of these locations also have been surveyed for mammals, including bats (Mac Nally et al. 2002). We have categorized all locations with respect to ecological vegetation classes using GIS-based maps of topography, soils, and geology and groundtruthing. We are in the process of collecting validation data from 80 new locations and from 40 of the original locations. Simultaneously, we are collaborating with the Victorian Department of Natural Resources and Environment and other stakeholders to develop a suite of alternative reconstruction scenarios.

Landscape reconstruction offers a potential means to mitigate pervasive losses of native species and promote future ecological sustainability. The focus of revegetation and other types of ecological restoration has usually been on either relatively small areas or reestablishment of ecosystem functions, such as releasing enough water at the appropriate point in time to support fish spawning in a river. The theoretical and conceptual basis for creating vegetational communities that will be sufficient in extent and geometry to support viable native populations of native wildlife, however, is relatively weak (Lindenmayer et al. 1990).

Our approach will bridge existing gaps between modeling current occurrence patterns of individual species and analyzing the costs and benefits of alternative future scenarios for landscape reconstruction. Our methods allow us to consider the potential effects on species of concern if a landscape were managed for a specified allocation and spatial configuration of various vegetation classes or land uses. For example, we can ask how the distribution of 1 or more endangered species might be affected if 25%, 60% or 90% of each presettlement ecological vegetation class was restored. Although our work has focused on native species, a similar process could be followed to predict the occurrence of non-native invasive species. We believe that our approach has promise for using ecological information to more effectively target conservation and restoration of locations with the greatest potential for achieving explicit biodiversity objectives.

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ORIGINAL ARTICLE

Comparative influence of spatial scale on beta diversity within regional assemblages of birds and butterflies

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ABSTRACT

Aim We examined whether variation in species composition of breeding birds and resident butterflies in the Great Basin of North America depended on sampling grain (the smallest resolvable unit of study) and on the relative proximity of sampling units across the landscape. We also compared patterns between the two taxonomic groups with reference to their life-history characteristics.

Location Data for our analyses were collected from 1996 to 2003 in three adjacent mountain ranges in the central Great Basin (Lander and Nye counties, Nevada, USA): the Shoshone Mountains, Toiyabe Range and Toquima Range.

Methods Data on species composition for both taxonomic groups were collecting using standard inventory methods for birds and butterflies in temperate regions. Data were compiled at three sampling grains, sites (average 12 ha), canyons (average 74 ha) and mountain ranges. For each sampling grain in turn, we calculated similarity of species composition using the Jaccard index. First, we investigated whether mean similarity of species composition among the three ranges differed as a function of the grain size at which data were compiled. Secondly, we explored whether mean similarity of species composition was greater for canyons within the same mountain range than for canyons within different mountain ranges. Thirdly, we examined whether mean similarity of species composition at the site level was different for sites within the same canyon, sites within different canyons in the same mountain range, and sites within canyons in different mountain ranges. We used a Bayesian model to analyse these comparisons.

Results For both taxonomic groups, mean similarity of species composition increased as the sampling grain increased. The effect of spatial grain was somewhat greater for birds than for butterflies, especially when the intermediate sampling grain was compared with the smallest sampling grain. Similarity of species composition of butterflies at each sampling grain was greater than similarity of species composition of birds at the same grain. Mean similarity of species composition of both birds and butterflies at the canyon level and site level was affected by relative proximity of sampling locations; beta diversity increased as the relative isolation of sampling locations increased.

Main conclusions The sensitivity of beta diversity to sampling grain likely reflects the effect of local environmental heterogeneity: as sampling grain increases, biotic assemblages appear more homogeneous. Although breeding birds in our study system have larger home ranges than resident butterflies, birds may have more specialized resource requirements related to vegetation structure and composition, especially at small sampling scales. The degree of variation in species composition of both taxonomic groups suggests that spatially extensive sampling

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will be more effective for drawing inferences about regional patterns of species diversity than intensive sampling at relatively few, smaller sites.

Keywords

Bayesian analyses, diversity patterns, Great Basin, Jaccard similarities, Nevada, proximity of samples, riparian areas, sampling grain, spatial scale, species composition.

INTRODUCTION

Measures of species diversity are dependent on spatial and temporal scale. For example, the size of each sampling unit, the spatial configuration or relative proximity of sampling units across the landscape, and the spatial extent of the area from which samples are drawn affect inferences about species richness and composition (Noss, 1983; Wilson & Shmida, 1984; Ricklefs & Schluter, 1993; Conroy & Noon, 1996; Reaka-Kudla *et al.*, 1997). Knowledge of relationships between species diversity and scale has wide-ranging application, from identification of appropriate boundaries for studying mechanisms that generate and maintain biological diversity (Kolasa, 1989, Rosenzweig, 1995, Underwood & Chapman, 1996; Willis & Whittaker, 2002), to prediction of how local and regional environmental changes will affect diversity at multiple levels of organization (Huston, 1994; Lockwood & McKinney, 2001; Scott *et al.*, 2002), to examination of relationships between species richness and ecological function (Waide *et al.*, 1999).

Most work on scaling issues associated with diversity patterns has concentrated on species richness. In part because counting species is logistically more feasible than collecting detailed demographic data, species richness has been used as a variable to help prioritize conservation efforts (Scott *et al.*, 1993; Environment Conservation Council, 2000; Pimm *et al.*, 2001; Roberts *et al.*, 2002) and to measure biological responses to natural disturbance processes, human land use, and alternative management actions at numerous spatial extents (Chapin *et al.*, 2000; Pressey *et al.*, 2000). Beta diversity (between-habitat diversity), which increases as a function of turnover in species composition among communities, most often has been considered in terms of its contribution to species richness of a heterogeneous landscape (MacArthur, 1965; Whittaker, 1977; Lande, 1996). For example, the method of additive partitioning uses a hierarchical model of landscape organization (Allen & Starr, 1982) to represent diversity at each nested level of a landscape as the sum of alpha (within-habitat) and beta diversity at the next lower level (Allan, 1975; Lande, 1996; Wagner *et al.*, 2000; Fournier & Loreau, 2001; Gering *et al.*, 2003). In other words, additive partitioning calculates the relative contributions of alpha and beta diversity to overall species richness at multiple spatial levels. In this paper, by contrast, we focus directly on whether beta diversity depends on sampling grain (the smallest resolvable unit of study, King, 1991; Morrison & Hall, 2002) and the proximity of sampling units across the landscape.

We also examine the taxonomic component of scaling issues. Species perceive and react to their environment as a function of their resource requirements, mobility, and other life-history characteristics (Addicott *et al.*, 1987; Kotliar & Wiens, 1990; Mac Nally, 2004). In theory, the grain of sampling and the extent of sampling (the area over which observations are made) should be dictated by the ecology of the species under investigation (Kotliar & Wiens, 1990; Mac Nally, 2004). In reality, however, sampling designs frequently reflect logistic constraints. Even if the optimal sampling regime for each major guild in a landscape has been identified, the grain and extent of sampling for multi-taxonomic studies commonly is established using a single convenient human perspective, such as administrative boundaries or land-use types. But a uniform sampling framework may not be meaningful for understanding diversity patterns in all taxonomic groups of interest (Addicott *et al.*, 1987; Kolasa, 1989), and sampling schemes can affect practical decisions about allocation of conservation funds and protected areas (Bassett & Edwards, 2003). Several studies have found low correlation in species richness among taxonomic groups at scales associated with local management (Prendergast *et al.*, 1993; Rubinoff, 2001). However, evidence on correlation in species richness among taxonomic groups at scales associated with ecoregional assessment is more equivocal (Olson & Dinerstein, 1998; Ricketts *et al.*, 1999; Stein *et al.*, 2000). Correlations between species richness of different taxonomic groups often increase as the spatial grain and extent of sampling increase (e.g. Swengel & Swengel, 1999).

The Great Basin of western North America is an excellent study system for exploring simultaneously the effects of spatial scale and taxonomic group on beta diversity. The Great Basin includes more than 425,000 km^2 of internal drainage extending from the Sierra Nevada in the west to the Wasatch Range in the east (Grayson, 1993). The topography of the region is dominated by more than 200 major mountain ranges, most with a north–south orientation, that were isolated from each other and from the surrounding lower-elevation valleys as the regional climate became warmer and drier following the Pleistocene (Brown, 1978; Wells, 1983; Grayson, 1993). Individual mountain ranges function as discrete habitat islands for many taxa that have relatively low mobility or cannot survive in the arid valleys (tens of km wide) separating the ranges, including birds and butterflies (McDonald & Brown, 1992; Murphy & Weiss, 1992). We recently found that turnover of species composition within sites over time accounted for much less of the difference in species composition of butterflies in the Great Basin than did spatial differences among sites (Fleishman & Mac Nally, 2003). Therefore, we decided it would be useful to explore relationships between beta diversity and spatial scale more thoroughly.

Numerous canyons incise the eastern and western slopes of mountain ranges in the Great Basin. For many species of birds and butterflies, canyons also represent archipelagos of habitat islands (Fleishman *et al.*, 1997; Fleishman & Murphy, 1999; Fleishman & Mac Nally, 2002). Although some animals may be physically capable of dispersing among canyons, movement often is deterred by canyon topography (frequently narrow and steeply-walled) and the dearth of resources and shelter from predators in the intervening uplands. Many of the breeding birds in our study system have territory sizes ranging from 4 to 40 ha (American Ornithologists' Union, 1992). By contrast, few of the resident butterflies regularly disperse more than a few hundred metres from where they eclosed (Fleishman *et al.*, 1997). Thus, movement within canyons probably is somewhat more common for birds than for butterflies. As a result, one might expect species composition of birds to be less variable in space than species composition of butterflies.

If one assumes that ecological specialization and geographical distribution are correlated (Rabinowitz, 1981; Kunin & Gaston, 1997), then one also might expect beta diversity to be greater among species with relatively specialized resource requirements than among relative generalists. Although birds initially might seem to have more general requirements than butterflies, this may not be the case in the Great Basin. In fact, previous work suggested that resource specialization was more strongly associated with structure of bird assemblages than was territory size (Fleishman *et al.*, 2002). Species composition of breeding birds in our study system may be affected by the patchy distribution of trees such as willow (*Salix* spp.), aspen (*Populus tremuloides*), and piñon (*Pinus monophylla*), which provide nesting sites that differ in their suitability for particular species or guilds (Fleishman *et al.*, 2003). Butterflies often are considered 'specialists' because they are restricted to one or a few closely related larval host plants (Ehrlich & Raven, 1965; Scott, 1986; Kremen, 1992; Blair & Launer, 1997). However, in many ecosystems, the resource requirements of adult butterflies are fairly general (Holl, 1995; Pullin, 1995). Many adult butterflies can exploit virtually any source of nectar, from flowering shrubs to native forbs to non-native invasive species. Previous work has shown that availability of nectar is positively correlated with spatial distribution of adults and larvae (Gilbert & Singer, 1973; Murphy, 1983; Murphy *et al.*, 1984) and may lessen local emigration (Kuussaari *et al.*, 1996; Moilanen & Hanski, 1998). Thus, species composition of butterflies in the Great Basin may be more closely associated with distribution of an array of potential nectar sources than with distribution of specific larval host plants.

In this paper, we examine whether variation in species composition of birds and of butterflies in the Great Basin depended on sampling grain (the smallest resolvable unit of study) and on the proximity of sampling units across the landscape. We also compare response of species composition to sampling grain and proximity between the two taxonomic groups with reference to their life-history characteristics.

METHODS

Field methods

Data for our analyses were collected from 1996 to 2003 in three adjacent mountain ranges in the central Great Basin, the Shoshone Mountains (1850 km^2, approximate north–south boundaries 39°14′19″ to 38°57′32″), Toiyabe Range (3100 km^2, approximate north–south boundaries 39°54′ to 38°30′), and Toquima Range (1750 km^2, approximate north–south boundaries 39°17′50″ to 38°29′9″) (Lander and Nye counties, Nevada, USA) (Fig. 1). These mountain ranges have similar regional climate, biogeographical past and ancestral biota, and human land-use histories (Wilcox *et al.*, 1986; Austin & Murphy, 1987; Grayson, 1993; Fleishman *et al.*, 2000).

Inventories for breeding birds were conducted in five canyons in the Shoshone Mountains, five canyons in the Toiyabe Range and six canyons in the Toquima Range. Inventories for resident butterflies were conducted in eight canyons in the Shoshone Mountains, 15 canyons in the Toiyabe Range and 11 canyons in the Toquima Range. Distances between canyons in these three mountain ranges, and particularly between the canyons we sampled, usually were much greater than the territory or home range sizes of birds (at least during the breeding season) (Ryser, 1985; Dobkin & Wilcox, 1986; American Ornithologists' Union, 1992) and resident butterflies (Fleishman *et al.*, 1997) in our study system.

We divided canyons into multiple contiguous sites (segments) from base to crest. Each site was 100 m wide and long enough to span a 100-m change in elevation (Fleishman *et al.*, 1998, 2001). Mean site length was 1.5 km; more than two-thirds of the sites were >1 km long. Inventories for birds were conducted from 2001 to 2003 in 24 sites in the Shoshone Mountains, 31 in the Toiyabe Range and 28 in the Toquima Range. Inventories for butterflies were conducted from 1995 to 2003 in 39 sites in the Shoshone Mountains, 102 in the Toiyabe Range and 54 in the Toquima Range.

Our sampling locations covered an elevational range of 1872–3272 m and areas from 1.5 to 44.4 ha. We followed standard inventory methods for birds and butterflies in temperate regions (Shapiro, 1975; Swengel, 1990; Pollard & Yates, 1993; Harding *et al.*, 1995; Bibby *et al.*, 2000). Birds were sampled during the breeding season (late May to June) using two or three 75-m fixed-radius point counts in each site.

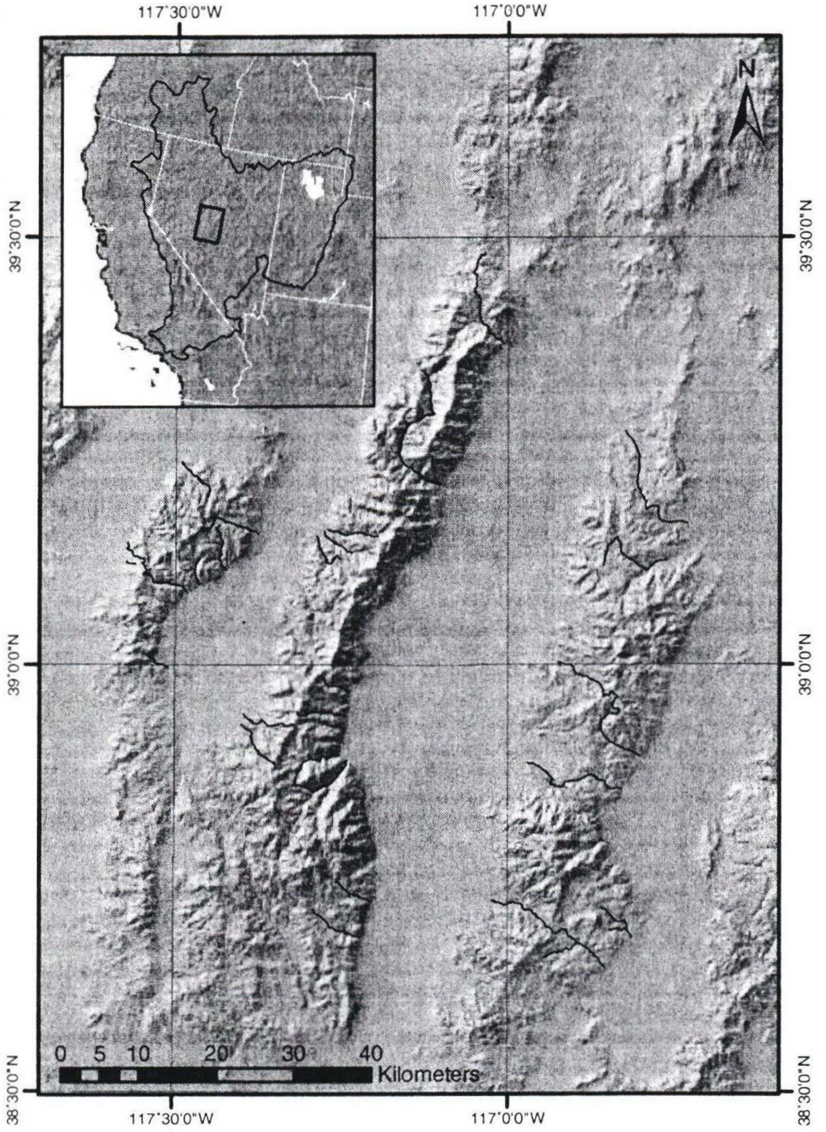

Figure 1 Location of the Shoshone Mountains, Toiyabe Range and Toquima Range in the Great Basin (black rectangle, see inset) and inventory canyons in the three mountain ranges (thick black lines). Two pairs of canyons in the Toiyabe Range and three pairs of canyons in the Toquima Range connect at the crest of the range.

Within a site, points were located in each of the dominant vegetation types (e.g. aspen, willow, piñon-juniper, wet meadow and sagebrush) to account for the influence of variables such as tree species composition, tree size, and water availability on avian species richness and composition (Betrus, 2002; Poulson, 2002). Each site included at least two point-count locations even if there was only one major vegetation type. Sites included three point-count locations when there were three different vegetation types within the site. Point count locations were at least 200 m apart.

Each time a point was surveyed, we recorded all birds actively using terrestrial habitat within the circle. During our inventories, birds displayed a variety of breeding behaviours including frequent song repetition by males, collection of nest material, nest building, incubation, parental care and territorial defence. Each point was visited three times during the breeding season. Point counts were conducted only under fair skies. Each point received at least one count within 2 h of dawn and at least one count between 2 and $3\frac{1}{2}$ h after dawn. No counts were conducted more than $3\frac{1}{2}$ h after dawn. Three surveys are considered sufficient to determine which species of birds are present at point count locations (Siegel *et al.*, 2001). In addition, point counts have been shown to be an effective method of sampling birds in riparian areas in the Great Basin (Dobkin & Rich, 1998). In our work, species accumulation curves for birds at the site and canyon levels generally approached an asymptote by the third round of surveys (Betrus, 2002). We recorded 79 species of breeding birds from our study sites. Complete data are available from the corresponding author on request.

We inventoried butterflies using walking transects, an established technique for temperate regions that reliably detects species presence and permits assessment of distributional trends across space and time (Pollard & Yates, 1993; Harding *et al.*, 1995). These methods have been described in considerable detail in previous publications (e.g. Fleishman *et al.*, 1998, 2000, 2001), so we present just a brief overview here. Approximately every 2 weeks throughout the majority of the flight season (late May to August – i.e. the period during which adult butterflies are present), using equal sampling effort per unit area, we recorded the presence of all butterfly species seen in each site. It is reasonable to interpret that a given butterfly species is absent if the area has been searched using these methods during the appropriate season and weather conditions (Pullin, 1995; Reed, 1996). In the Toiyabe Range, for example, we recorded 98% of the theoretical number of species expected under a Michaelis–Menten model (Clench, 1979; Raguso & Llorente-Bousquets, 1990; Soberón & Llorente, 1993; Fleishman *et al.*, 1998). Sites were sufficiently large relative to the home ranges of resident butterflies in the region that the short-term presence of butterfly species in each site was independent (i.e. an individual was not recorded in >1 site during an inventory round) (Fleishman *et al.*, 1997). We recorded 65 resident species of butterflies from our study sites. Complete data are available from the corresponding author on request.

Analyses

Our smallest sampling grain was the site. A given site was located within a particular canyon within one of the three mountain ranges. In assessing faunal similarity, we could compare the species composition of birds or butterflies in any one site with the species composition in any other site. There were three possibilities with respect to the relative proximity of two sites. First, both sites could be located within the same canyon ($\pi_{\text{within-canyons}}$). Secondly, the two sites could be in different canyons within the same mountain range ($\pi_{\text{among-canyons}}$). Thirdly, the sites could be located in canyons in different mountain ranges ($\pi_{\text{among-ranges}}$). The number of species was the same for all spatial arrangements (79 species of birds, 65 species of butterflies).

To produce species lists at the whole canyon level, our intermediate sampling grain, we compiled species lists for all contiguous sites within a given canyon. On average, the area of a canyon was six times larger than the area of a site. There were two possibilities with respect to the relative proximity of two canyons. First, two canyons might be located within the same mountain range ($\chi_{\text{within-ranges}}$). Secondly, the canyons could be in different mountain ranges ($\chi_{\text{among-ranges}}$). To produce species lists at the mountain range level, our largest sampling grain, we compiled species lists for all canyons that were visited in a given mountain range. We could then calculate similarity of species composition among mountain ranges ($\rho_{\text{among-ranges}}$). Data at the mountain range level were less exhaustive than data for canyons or sites. Although we included the majority of accessible canyons in our inventories, especially for butterflies, some canyons in each mountain range were too remote or impenetrable to be visited on a regular basis. Inventories for birds were constrained by the number of locations that could be visited in the early morning hours during the breeding season.

For each sampling grain in turn – sites, canyons and mountain ranges – we calculated similarity of species composition using the Jaccard index, $C_J = j/(a+b-j)$, where j is the number of species found in all locations and a and b are the number of species in locations A and B, respectively. C_J is 1.0 when species composition is identical between locations and 0.0 when two locations have no species in common (Magurran, 1988).

We conducted three analyses on the sets of similarity values for sites, canyons and mountain ranges. First, we investigated whether mean similarity of species composition among the three ranges differed as a function of the grain size at which data were compiled:

$$\pi_{\text{among-ranges}} \text{ vs. } \chi_{\text{among-ranges}} \text{ vs. } \rho_{\text{among-ranges}}.$$

Secondly, we explored whether mean similarity of species composition was greater for canyons within the same mountain range than for canyons within different mountain ranges:

$$\chi_{\text{among-ranges}} \text{ vs. } \chi_{\text{within-ranges}}.$$

Thirdly, we examined whether mean similarity of species composition at the site level was different for sites within the same canyon, sites within different canyons in the same mountain range, and sites within canyons in different mountain ranges:

$$\pi_{\text{within-canyons}} \text{ vs. } \pi_{\text{among-canyons}} \text{ vs. } \pi_{\text{among-ranges}}.$$

We used a simple Bayesian approach to quantify these comparisons. One of the advantages of this approach was that it provided credible intervals for differences between mean similarities of species composition. Credible intervals summarize the state of uncertainty concerning the value of the fixed constant – the parameter's true value – about which our sample provides information. Thus, one often uses '95% Bayesian credible intervals' (Lee, 1989) to characterize the range of values for the parameter that encompasses 95% of the probability mass for that parameter. Credible intervals are conceptually distinct from the frequentist confidence interval, the interpretation of which depends on the theoretical possibility of repeating an experiment or survey many times, which is rarely possible in biogeographical studies (e.g. there is only one Shoshone Mountains, one Toiyabe Range and one Toquima Range).

The basic model we used was

$$Y_{ij} = \mu_0 + \zeta_i, \quad Y_{ij} \sim \text{Norm}(\mu_i, \sigma^2_{\text{within}}); \quad \mu_i \sim \text{Norm}(\mu_i, \sigma^2_{\text{between}}).$$

In this model, the Y_{ij} are the similarities of species composition between a pair of sampling units at any spatial grain (sites, canyons or mountain ranges), μ_0 is the intercept, and ζ_i is the effect of 'treatment' i. Treatments were alternative proximities of locations, e.g. sampling units within the same mountain range vs. sampling units in different mountain ranges, and there were either two or three treatments depending on which spatial grain was being examined (two for mountain ranges and canyons, three for sites; see above). The intercept was 'aliased' with the first treatment, so that the ζ_i for the second (and, in some cases, third) treatment(s) was expressed relative to the first treatment (i.e. $\zeta_1 \equiv 0$). For example, if $\mu_0 = 0.3$ and $\zeta_2 = 0.2$, then the mean of the first treatment was estimated to be 0.3 and the mean of the second treatment was $\mu_0 + \zeta_2 = 0.3 + 0.2 = 0.5$.

The Y_{ij}s are imperfect measurements assumed to represent Normally distributed unknown fixed means μ_i with a common variance. We computed variance components for between treatments ($\sigma^2_{\text{between}}$) and within treatments (σ^2_{within}).

Software and statistical decision criteria

We used the WinBUGS Bayesian analysis program (version 1.4, Spiegelhalter *et al.*, 2003). The Bayesian approach to estimating parameters formally incorporates prior knowledge about the values of a parameter and produces a probability statement about the interval within which the parameter value lies. This means that each regression coefficient will have a distribution of values rather than a single value. If one has no prior knowledge about the values of a parameter, then it is appropriate to use a 'non-informative' prior distribution for that parameter. One might use a flat uniform distribution (between two endpoints, ±1000 perhaps) or a Normal distribution with high variance (mean = 0, variance = 200, perhaps). Use of non-informative priors when there is little or no prior information means that the posterior probability distributions are dictated by the newly collected data (Lee, 1989). In this study, we used non-informative, Normal priors for all parameters because we had no prior information about how mean similarity of species composition of birds and butterflies varied as a function of spatial grain or relative proximity of sampling units. In all analyses, means and medians of posterior distributions of parameters were similar, indicating symmetric probability distributions.

Bayesians eschew significance tests using the null-hypothesis–*P*-value framework. Nevertheless, there is a sophisticated field of Bayesian decision-making using Bayes factors (Spiegelhalter & Smith, 1982; Gelman *et al.*, 1995) and decision theory (Bernardo & Smith, 1994; Jaynes, 2003). We took a simple approach in which our decision criterion for whether there were 'substantial' differences among treatments was whether differences in model coefficients had a high (> 90%) posterior probability of being greater than or less than zero. Bayesian calculations provide a probability distribution for each model parameter (and combinations thereof, such as differences between any two parameters), and one can compute how much of this distribution lies above or below zero. For example, for a parameter with a negative mean, 78% of the probability mass might lie below zero and 22% above zero. Because 78% < 90%, we regarded the values as providing only limited evidence that the parameter was sufficiently 'far' from zero to be an important effect. However, if 93% of the probability mass were below zero, then this provided stronger evidence that the effect associated with the parameter indeed was important. For parameters (or functions of parameters) with positive means, the fraction of the probability mass above zero was used as the criterion. Note that use of a decision criterion, as with a significance level, is arbitrary. However, because our data were Normally distributed, readers can select a different decision criterion, such as > 75% or > 95%, that they believe to be more appropriate.

RESULTS

To avoid potential confusion, note that the mean ± SD values cited in the text are the sample means and SDs computed from the Jaccard similarities, without reference to the Bayes model. Sample means are not expressed relative to the first treatment (see Methods). Values in the accompanying tables are parameter means (±SDs) from the Bayes model, and are expressed relative to the first treatment. Percentages in the text were calculated using parameter means.

Similarity of species composition among mountain ranges as a function of sampling grain: $\pi_{\text{among-ranges}}$ vs. $\chi_{\text{among-ranges}}$ vs. $\rho_{\text{among-ranges}}$

Birds

First, we explored whether similarity of species composition of birds among mountain ranges differed as a function of sampling grain. We found that mean similarity of species composition increased as the sampling grain increased: $\pi_{\text{among-ranges}} < \chi_{\text{among-ranges}} < \rho_{\text{among-ranges}}$. Mean similarity of species composition of birds among mountain ranges was 117% higher when measured at the spatial grain of mountain ranges (ρ) (0.662 ± 0.068 SD) than at the spatial grain of sites (π) (0.295 ± 0.126 SD) (percentage calculated using parameter means in Table 1). Likewise, mean similarity of species composition of birds among mountain ranges was 69% higher when measured at the spatial grain of canyons (χ) (0.498 ± 0.088 SD) than at the spatial grain of sites (π). These differences were deemed substantial using our Bayesian decision criterion [posterior probability mass (PPM) column in Table 1]. About 85% (median 88%) of the variation in the similarity values was attributable to differences in sampling grain; we provide median estimates for these variance proportions because of their asymmetric (Gamma) probability distributions (Table 1).

Butterflies

Similarity of species composition of butterflies among mountain ranges, like birds, differed as a function of sampling grain, with mean similarity of species composition increasing as the sampling grain increased. However, similarity of species composition of butterflies at each sampling grain was greater than similarity of species composition of birds at the same grain (Tables 1 & 2). At the smallest grain,

Table 1 Bayesian comparisons of differences in mean similarity of species composition of birds at three sampling grains in increasing order of size: sites, canyons, and mountain ranges. μ_0 is the intercept, and ζ_i is the effect of each 'treatment' i – an alternative spatial configuration (relative proximity) of sampling units. ζ_i for the second and third treatments are expressed relative to the first treatment. Thus, the mean of the second treatment was 0.295 + 0.203 = 0.498, and the mean of the third treatment was 0.295 + 0.344 = 0.639. $\sigma^2_{\text{between}}$ is the variance component between treatments and σ^2_{within} is the variance component within treatments. Values for the lowest 2.5% of the posterior probability distribution of each quantity fell below the 2.5% credible interval, and values for the upper 2.5% of the probability distribution of each quantity fell above the 97.5% credible interval. The posterior probability mass (PPM) shows the fraction of the probability distribution that lay above zero. PPM > 0.9 (for positive means) or < 0.1 (for negative means) were considered substantial – i.e. evidence that the effect was important

Quantity	Parameter mean ± SD	Credible interval		PPM
		2.5%	97.5%	
μ_0: sites (n = 3486)	0.295 ± 0.002	0.291	0.299	–
ζ_2: canyons (n = 120)	0.203 ± 0.012	0.179	0.227	1
ζ_3: ranges (n = 3)	0.344 ± 0.074	0.204	0.492	1
$\zeta_2 - \zeta_3$	−0.142 ± 0.075	−0.288	0.006	0.03
$\sigma^2_{\text{between}}$ (proportion)	0.846 ± 0.122*	0.570	0.994	–
σ^2_{within} (proportion)	0.154 ± 0.122†	0.008	0.442	–

Medians: *0.876, †0.125.

Values in the text are sample means rather than means obtained from the Bayes model.

sites (π), mean similarity of species composition of butterflies was 0.397 ± 0.132 SD. At the intermediate grain, canyons (χ), mean similarity of species composition of butterflies was 0.581 ± 0.136 SD. At the largest sampling grain, mountain ranges (ρ), mean similarity of species composition of butterflies was 0.875 ± 0.079 SD. The difference in values among spatial grains was substantial on the basis of our Bayesian decision criterion (Table 2). More than 88% of the variance in mean similarity of species composition was attributable to difference in relative proximity of sampling units (Table 2).

Similarity of species composition among canyons as a function of relative proximity:

$\chi_{\text{among-ranges}}$ vs. $\chi_{\text{within-ranges}}$

Birds

We investigated whether similarity of species composition of birds among canyons differed as a function of relative proximity – whether mean similarity of species composition was greater for canyons within the same mountain range than for canyons within different mountain ranges. Mean similarity of species composition of birds among pairs of canyons within the same mountain range (0.554 ± 0.074 SD) was 14% greater than mean similarity of species composition of birds among pairs of canyons in different mountain ranges (0.474 ± 0.082 SD); this difference was substantial using our Bayesian decision criterion (Table 3). The majority of the variance in mean similarity of species composition (69%) was associated with relative proximity (the treatment difference) (Table 3).

Butterflies

Results for butterflies were similar to those for birds. Similarity of species composition of butterflies among canyons differed as a function of relative proximity. Mean similarity of species composition of butterflies among pairs of canyons within the same mountain range (0.615 ± 0.137 SD) was about 8% greater than mean similarity of species composition among pairs of canyons in different mountain ranges (0.564 ± 0.132 SD); this difference was substantial (Table 4). However, in this analysis, unlike previous analyses, less than 50% of the variance

Table 2 Bayesian comparisons of differences in mean similarity of species composition of butterflies at three sampling grains in increasing order of size: sites, canyons and mountain ranges

Quantity	Parameter mean ± SD	Credible interval		PPM
		2.5%	97.5%	
μ_0: sites (n = 18,916)	0.397 ± 0.001	0.396	0.399	–
ζ_2: canyons (n = 561)	0.184 ± 0.005	0.173	0.195	1
ζ_3: ranges (n = 3)	0.457 ± 0.078	0.306	0.613	1
$\zeta_2 - \zeta_3$	−0.273 ± 0.078	−0.425	−0.117	0
$\sigma^2_{\text{between}}$ (proportion)	0.881 ± 0.103*	0.630	0.997	–
σ^2_{within} (proportion)	0.119 ± 0.103†	0.003	0.375	–

PPM, posterior probability mass.

Medians: *0.907, †0.093.

Table 3 Bayesian comparisons of differences in mean similarity of species composition of birds at the intermediate sampling grain (canyons), with two different relative proximities: canyons within the same mountain range and canyons in different mountain ranges

Quantity	Parameter mean ± SD	Credible interval		PPM
		2.5%	97.5%	
μ_0: within ranges (n = 35)	0.553 ± 0.014	0.525	0.580	–
ζ_2: among ranges (n = 85)	−0.078 ± 0.017	−0.110	−0.045	0
$\sigma^2_{\text{between}}$ (proportion)	0.692 ± 0.255*	0.183	1.000	–
σ^2_{within} (proportion)	0.308 ± 0.255†	0.001	0.821	–

PPM, posterior probability mass.

Medians: *0.752, †0.250.

Table 4 Bayesian comparisons of differences in mean similarity of species composition of butterflies at the intermediate sampling grain (canyons), with two different relative proximities: canyons within the same mountain range and canyons in different mountain ranges

Quantity	Parameter mean ± SD	Credible interval 2.5%	97.5%	PPM
μ_0: within ranges (n = 187)	0.616 ± 0.010	0.596	0.636	–
ζ_2: among ranges (n = 374)	−0.051 ± 0.013	−0.076	−0.026	0
$\sigma^2_{\text{between}}$ (proportion)	0.438 ± 0.311*	0.042	0.996	–
σ^2_{within} (proportion)	0.562 ± 0.311†	0.004	0.958	–

PPM, posterior probability mass.
Medians: *0.358, †0.643.

in mean similarity of species composition (44%, median 36%) was attributable to relative proximity or 'treatment' (Table 4).

Similarities of species composition among sites as a function of relative proximity: $\pi_{\text{within-canyons}}$ vs. $\pi_{\text{among-canyons}}$ vs. $\pi_{\text{among-ranges}}$

Birds

Mean similarity of species composition of birds among sites varied as a function of the relative proximity of those sites: $\pi_{\text{within-canyons}} > \pi_{\text{among-canyons}} > \pi_{\text{among-ranges}}$. Mean similarity of species composition of birds among pairs of sites within the same canyon (0.379 ± 0.156 SD) was about 8% greater than mean similarity of species composition among pairs of sites in different canyons in the same mountain range (0.348 ± 0.138 SD). The greatest difference in species composition of birds occurred among sites in different mountain ranges (0.267 ± 0.107 SD). Similarity of species composition of birds among sites in different mountain ranges was 30% less than similarity among sites within the same canyon. Differences in relative proximity were substantial (Table 5). About 38% of the variance in similarities was attributable to relative proximity of sampling units (Table 5).

Butterflies

Results for butterflies were similar to results for birds: $\pi_{\text{within-canyons}} > \pi_{\text{among-canyons}} > \pi_{\text{among-ranges}}$. Mean similarity of species composition of butterflies among pairs of sites within the same canyon (0.523 ± 0.156 SD) was *c.* 20% greater than mean similarity of species composition among pairs of sites in different canyons in the same mountain range (0.419 ± 0.140 SD) and *c.* 28% greater than mean similarity of species composition among pairs of sites in different mountain ranges (0.379 ± 0.120 SD). Both differences were substantial using our Bayesian decision criterion (Table 6). About 42% of the variation in similarity of species composition was attributable to relative proximity (Table 6).

Table 5 Bayesian comparisons of differences in mean similarity of species composition of birds at the smallest sampling grain (sites), with three different relative proximities: sites in different canyons in the same mountain range, sites in different mountain ranges, and sites within the same canyon

Quantity	Parameter mean ± SD	Credible interval 2.5%	97.5%	PPM
μ_0: among canyons (n = 951)	0.347 ± 0.004	0.340	0.354	–
ζ_2: among ranges (n = 2343)	−0.080 ± 0.005	−0.098	−0.072	0
ζ_3: within canyons (n = 192)	0.031 ± 0.009	0.012	0.050	1
$\zeta_2 - \zeta_3$	−0.112 ± 0.009	−0.128	−0.092	0
$\sigma^2_{\text{between}}$ (proportion)	0.377 ± 0.237*	0.080	0.923	–
σ^2_{within} (proportion)	0.624 ± 0.237†	0.080	0.920	–

PPM, posterior probability mass.
Medians: *0.306, †0.695.

Table 6 Bayesian comparisons of differences in mean similarity of species composition of butterflies at the smallest sampling grain (sites), with three different relative proximities: sites in different canyons in the same mountain range, sites in different mountain ranges, and sites within the same canyon

Quantity	Parameter mean ± SD	Credible interval 2.5%	97.5%	PPM
μ_0: among canyons (n = 6772)	0.419 ± 0.002	0.415	0.422	–
ζ_2: among ranges (n = 11,592)	−0.040 ± 0.002	−0.043	−0.036	0
ζ_3: within canyons (n = 555)	0.104 ± 0.006	0.093	0.115	1
$\zeta_2 - \zeta_3$	−0.143 ± 0.006	−0.155	−0.132	0
$\sigma^2_{\text{between}}$ (proportion)	0.419 ± 0.232*	0.107	0.938	–
σ^2_{within} (proportion)	0.581 ± 0.232†	0.063	0.893	–

PPM, posterior probability mass.
Medians: *0.366, †0.664.

DISCUSSION

We found that variation in species composition of birds and of butterflies in the Great Basin depended on both sampling grain (the smallest resolvable unit of study) and on the relative proximity of sampling units across the landscape. At all three sampling grains, species composition of butterflies was more similar than species composition of birds. The effect of spatial grain was greater for birds than for butterflies, especially when the intermediate sampling grain was compared with the smallest sampling grain. The effects of relative proximity of sampling units across the landscape were not uniformly greater for either taxonomic group.

Sampling grain

Species composition of both birds and butterflies varied as a function of sampling grain (the smallest resolvable unit of study). Similarity of species composition increased as the sampling grain increased, and the majority of variation in similarity values (*c.* 85% for birds, 88% for butterflies) was attributable to sampling grain. This result almost certainly reflects the effect of local environmental heterogeneity on species composition. Species composition within a canyon may respond to differing distributions of resources or microclimatic features along an elevational gradient. As sampling resolution increases, biotic assemblages appear more homogeneous (i.e. similarity of species composition between two assemblages increases). Within a mountain range, the distribution of resources along an elevational gradient may be similar among canyons (Fleishman *et al.*, 2003). At the mountain range level, species composition may reflect emerging similarities in terms of regional climate, land cover and land use.

Relative proximity

We examined the effects of relative proximity of sampling units at two different grains – canyons and sites. Irrespective of grain size or taxonomic group, similarity of species composition decreased as the biogeographical separation between sampling units increased. At the canyon grain, the effect of relative proximity was considered substantial using the Bayesian decision criterion. However, the absolute difference in species composition in response to relative proximity was modest – assemblages of birds were 14% more similar, and assemblages of butterflies were 8% more similar, when canyons were located in the same mountain range than when canyons were located in different mountain ranges. These results and our personal observations concur with the remarks of previous workers (e.g. Dobkin & Wilcox, 1986) that even within the same mountain range, canyon physiography is extremely variable. Although there are relatively few major land cover types in the Great Basin, they are distributed in a remarkable array of local vegetational mosaics. Canyons in relatively dry mountain ranges usually have more depauperate assemblages of plants and animals than canyons in relatively mesic mountain ranges, yet almost every canyon remains an 'island' with a distinct character. Thus, a randomly selected pair of canyons within the same mountain range may not be much more similar than a randomly selected pair of canyons from two nearby mountain ranges.

At the smallest grain (sites), the effect of relative proximity was again (statistically) substantial but less than expected, especially within a mountain range. Mean similarity of species composition of birds among sites within the same canyon was only *c.* 8% greater than among sites in different canyons in the same mountain range. Relative proximity had a stronger effect on similarity of butterfly assemblages (20% greater among sites within the same canyon than among sites in different canyons in the same mountain range). A likely explanation may be, as noted above, that species composition within a canyon reflects local environmental heterogeneity – the distribution of resources for birds and butterflies often shifts along an elevational gradient (Fleishman *et al.*, 1998, 2000). Two sites within the same canyon are more similar than two sites within different canyons, but the resemblance is not necessarily close. The magnitude of the difference in species composition increased as we compared sites within a canyon to sites in different ranges. The latter result may be associated with broad, mountain range-level differences in moisture and associated resource availability.

Taxonomic group

As we compare the effects of spatial grain and relative proximity on beta diversity of birds and butterflies, two differences immediately are apparent. First, at all spatial grains (sites, canyons and mountain ranges), species composition of butterflies was more similar than species composition of birds. At the smallest grain (sites), mean similarity of species composition of butterflies was 10% higher than that of birds. The difference was 8% at the intermediate grain (canyons) and 21% at the largest grain (mountain ranges). Secondly, although the difference in species composition at the largest vs. intermediate grains was very similar for both taxonomic groups, there was noticeably (23%) more difference in species composition of birds than of butterflies at the intermediate grain vs. the smallest grain.

Breeding birds in our study system typically have territory sizes or home ranges about an order of magnitude larger than resident butterflies (American Ornithologists' Union, 1992; Fleishman *et al.*, 1997). If home range size is the primary influence on species composition, then beta diversity of birds should be lower than beta diversity of butterflies. If resource requirements are influential, then beta diversity of taxonomic groups with relatively general needs should be lower than beta diversity of groups with more specialized needs.

Species composition of birds has been thought to be more closely associated with vegetation structure (physiognomy) than with vegetation composition (floristics) (MacArthur *et al.*, 1966; Anderson & Shugart, 1974; Rotenberry & Wiens, 1980). However, some evidence suggested that vegetation composition is more influential than vegetation structure (Tomoff, 1974; Power, 1975; Wiens & Rotenberry, 1981), especially at relatively small spatial grains and extents (Rotenberry, 1985; Wiens *et al.*, 1987). As we noted in the Introduction, most species of trees in our study system have heterogeneous distributions. Piñon (*P. monophylla*) and juniper (*Juniperus osteosperma*) are relatively widespread and sometimes form large stands, especially in drier areas. However, riparian trees and shrubs such as cottonwood and aspen (*Populus* spp.), willow (*Salix* spp.), chokecherry (*Prunus virginiana*), elderberry (*Sambuca* spp.), birch (*Betula occidentalis*), and rose (*Rosa woodsii*) have relatively patchy distributions, even in canyons with permanent sources of running or standing water. Neotropical migrant birds in particular (about one-third of the species of birds we recorded winter in the neotropics, Gough *et al.*, 1998) are thought to be relatively selective in choosing nesting sites because of the physical stress they undergo during migration and the limited temporal window available for establishing a breeding territory and reproducing (Robbins *et al.*, 1989; Martin, 1992, 1995). Year-round residents tend to be less selective. Most Neotropical migrants are insectivores, for example, while most year-round residents must exploit a greater range of food sources because insects are not available during the winter.

As spatial scale increases, the strength of the correlation between floristics and physiognomy may also increase (Mac Nally *et al.*, 2002). In addition, at larger spatial scales, species composition of birds, butterflies, and their resources may exhibit similar responses to abiotic environmental gradients (Hawkins & Porter, 2003). It is possible that for birds, the scale at which species distributions reflect sensitivity to floristics, vegetational heterogeneity, or both that lies somewhere between the site (canyon segment) level and the canyon level.

A similarity in the response of beta diversity of birds and butterflies to sampling grain also stands out: at small spatial grains, and even at intermediate sampling grains, variation in species composition was considerable. At the smallest grain, mean similarities of species composition of birds and butterflies were 0.295 and 0.397, respectively; at the intermediate grain, mean similarities were 0.498 for birds and 0.581 for butterflies. At the largest grain, mean similarities were 0.662 for birds and 0.875 for butterflies. In ecosystems with appreciable heterogeneity in physiography and land cover, turnover in species composition across a range of spatial scales is an important component of diversity patterns. Our results suggest that spatially extensive sampling may be a more effective strategy than sampling small areas scattered across the landscape for drawing inferences about regional species composition.

Ecologists are well aware that measures of species diversity, and inferences about diversity patterns, depend on spatial and temporal scale. Our work examined alternative hypotheses about sensitivity of birds and butterflies to the size of sampling units (spatial grain or resolution) and to the relative proximity of sampling units across the landscape. Contrary to expectations based on relative home range size of taxonomic groups, we found that assemblages of birds were more variable in space than assemblages of butterflies. Our results suggest that nesting and food resources may have considerable influence on beta diversity of birds, while the distribution of adult food resources appears to have a strong influence on beta diversity patterns of butterflies. Although the species composition of potential nectar sources varies in space, those resources often are relatively widespread. Field tests of diversity theories have great value for ecology and conservation. As our understanding of relationships between species diversity and various components of 'scale' increases, so should our ability to recognize underlying mechanisms. Such knowledge also increases our ability to make decisions about land use and land management that will allow us to maximize native biological diversity and ecological integrity.

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Using Indicator Species to Predict Species Richness of Multiple Taxonomic Groups

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Abstract: *Values of species richness are used widely to establish conservation and management priorities. Because inventory data, money, and time are limited, use of surrogates such as "indicator" species to estimate species richness has become common. Identifying sets of indicator species that might reliably predict species richness, especially across taxonomic groups, remains a considerable challenge. We used genetic algorithms and a Bayesian approach to explain individual and combined species richness of two taxonomic groups as a function of occurrence patterns of indicator species drawn from either both groups or one group. Genetic algorithms iteratively screen large numbers of potential models and predictor variables in a process that emulates natural selection. The best-fitting models of bird species richness and butterfly species richness explained approximately 80% of deviances and included only indicator species from the same taxonomic group. Using species from both taxonomic groups as potential predictors did not improve model fit but slightly improved the parsimony (fewer predictors) of the model of bird species richness. The best model of combined species richness included five butterflies and one bird and explained 83% of deviance, whereas a model of combined species richness based on six butterflies as indicators explained 82% of deviance. A model of combined species richness based on birds alone explained 72% of deviance. We found that a small, common set of species could be used to predict separately the species richness of multiple taxonomic groups. We built models explaining approximately 70% of the deviance in species richness of birds and butterflies based on a common set of three bird species and three butterfly species. We also identified a set of six species of butterflies that predicted ≥66% of both bird species richness and butterfly species richness. Our approach is applicable to any assemblage or ecosystem, and may be useful both for estimating species richness and for gaining insight into mechanisms that influence diversity patterns.*

Key Words: Bayes information criterion, bird species richness, butterfly species richness, genetic algorithm, Great Basin, land cover, land use, species occurrence

Utilización de Especies Indicadoras para Predecir la Riqueza de Especies de Múltiples Grupos Taxonómicos

Resumen: *Los valores de riqueza de especies son ampliamente utilizados para definir prioridades de conservación y manejo. Debido a que los datos de inventarios, el dinero y el tiempo son limitados, se ha vuelto común el uso de sustitutos, como las especies "indicadoras," para estimar la riqueza de especies. La identificación de conjuntos de especies indicadoras que pronostiquen la riqueza de especies confiablemente, especialmente en varios grupos taxonómicos, es un reto importante. Utilizamos algoritmos genéticos y un método Bayesiano para explicar las riquezas de especies individuales y combinadas de dos grupos taxonómico como una función de patrones de ocurrencia de especies indicadoras extraídas de ambos grupos o de uno. Los algoritmos genéticos reiterativamente filtran grandes números de modelos potenciales y variables predictoras en un proceso que*

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emula a la selección natural. Los modelos que mejor se ajustaron a la riqueza de especies de aves y de mariposas explicaron aproximadamente 80% de las anormalidades e incluyeron solo a especies indicadoras del mismo grupo taxonómico. Utilizando a especies de ambos grupos taxonómicos como predictores potenciales no mejoró el ajuste del modelo pero mejoró ligeramente la parsimonia (menos predictores) del modelo de riqueza de especies de aves. El mejor modelo de la riqueza de especies combinada incluyó a cinco especies de mariposas y una de ave y explico 83% de la anormalidad, mientras que un modelo de riqueza de especies combinadas basada en seis especies de mariposas explico 82% de la anormalidad. Un modelo de riqueza de especies combinadas basado solo en aves explicó 72% de la anormalidad. Encontramos que un conjunto pequeño, común, podría ser utilizado para pronosticar, por separado, la riqueza de especies de múltiples grupos taxonómicos. Construimos modelos que explicaron aproximadamente 70% de la anormalidad en la riqueza de especies de aves y mariposas con base en un conjunto común de tres especies de aves y tres de mariposas. También identificamos un conjunto de seis especies de mariposas que predijeron ≥ 66% de la riqueza de especies tanto de aves como de mariposas. Nuestro método es aplicable a cualquier ensamble o ecosistema, y puede ser útil tanto para estimar la riqueza de especies como para incrementar el entendimiento de los mecanismos que influyen sobre los patrones de diversidad.

Palabras Clave: algoritmo genético, cobertura de terreno, criterio Bayesiano de información, Great Basin, ocurrencia de especies, riqueza de especies de aves, riqueza de especies de mariposas, uso de suelos

Introduction

Protection of locations with a relatively large number of native species is thought to be an efficient way to maintain overall biodiversity (Scott et al. 1987; Myers et al. 2000). Data on species richness have supported a range of high-profile conservation efforts, particularly when information on endemism and changes in land use and land cover has also been available (Mittermeier et al. 1998; Hobohm 2003; Kareiva & Marvier 2003). Whether protection of locations containing large numbers of species has been effective in achieving broad conservation goals remains an open question (Christensen 2003), but extensive use of species richness as a criterion for development of conservation and management strategies almost certainly will continue.

Given that inventory data for many regions are sparse and acquisition of new data is costly, surrogate-based approaches to estimate species richness from data on land cover, land use, climate, and topography have become common (e.g., Mayer & Laudenslayer 1988; Boyce & McDonald 1999; Scott et al. 2002). Work also has been done to build functional relationships between species richness and the occurrence of "indicator" species (Pearson 1994; Scott 1998; Gustafsson 2000), which we define as a small set of species with presence or absence patterns that are correlated functionally with species richness of a larger group of organisms. If validation data sets demonstrate that the functions are effective, then—depending on the target system—it may be far more feasible to measure occurrence of indicator species than to conduct comprehensive species inventories (Gustafsson 2000).

A central challenge in predicting species richness as a function of indicator species is finding good sets of indicators. Selection of potential indicators through statistically based methods is most likely to be effective, especially when compared with selection based on ad hoc criteria such as a species' charisma or its legal protection status (Landres et al. 1998; Andelman & Fagan 2000; Mac Nally et al. 2000). An additional question is whether species from one taxonomic group (e.g., butterflies) might serve as indicators of the species richness of other taxonomic groups (e.g., herptiles or birds). Life-history characteristics that affect how species perceive and react to environments (Kotliar & Wiens 1990; Mac Nally 2005) are likely to be more different among than within major taxonomic groups. Therefore, it seems reasonable to assume that species richness of a given taxonomic group will be predicted more accurately on the basis of species drawn from that same taxonomic group than from a different taxonomic group. But conservation biologists have not quantified the magnitude of difference in predictive ability between indicators drawn from the same taxonomic group against indicators drawn from a different taxonomic group. Nor have they shown whether the fit of models of species richness for one taxonomic group can be improved by including indicator species from a second taxonomic group.

Accordingly, we addressed six related objectives concerning within-taxon and among-taxon models of species richness based on indicator species. First, we examined whether models of species richness for one taxonomic group could be improved by including indicator species from a second taxonomic group. Second, we quantified the fit of models of species richness for one taxonomic group based on indicator species drawn exclusively from a different taxonomic group. Third, we evaluated whether models of the combined species richness of two taxonomic groups could be built based on indicator species drawn either from both of those groups or exclusively from one of the groups. Fourth, we assessed whether the same set of indicator species could be used to predict species richness of two different taxonomic groups. Fifth, we explored whether taxonomic groups differ consistently in their ability to serve as indicators of species richness. Last, we considered the ecological characteristics of selected indicator species to gain insight into why the selected species might convey information about species richness.

We used the general statistical methodology developed by Mac Nally and Fleishman (2002, 2004) to identify indicators of species richness. This approach proved highly successful in a recent case study, in which a model based on the occurrence of five butterfly species explained 88% of the deviance of species richness of 56 species of butterflies in a mountain range in western North America (Mac Nally & Fleishman 2002). Validation tests showed that predicted and observed values of species richness were highly correlated, with 93% of the observed values falling within the 95% Bayesian-credible intervals of the predictions (Mac Nally & Fleishman 2004). Here, we extend this approach by employing a genetic algorithm to select indicator species from a set of potential indicators (139 total) that is too large to be evaluated using exhaustive search methods. Genetic algorithms are heuristic, iterative search procedures that emulate the process of natural selection. They are useful for large combinatory problems and have been used successfully to select input variables in neural networks (Jefferson et al. 1997) and logistic regression models (Vinterbo & Ohno-Machado 1999). The software we used also allowed for modeling based on Poisson errors, which is most appropriate for the numerical distribution of species richness (i.e., non-negative integers).

Methods

Field Methods

Data for our analyses were collected from 1996–2003 in three adjacent mountain ranges in the central Great Basin (Lander and Nye counties, Nevada, U.S.A.) that have similar biogeographic and human land-use histories, the Shoshone Mountains (1850 km^2, approximate north-south boundaries 39°14′19″ to 38°57′32″); the Toiyabe Range (3100 km^2, 39°54′00″ to 38°30′0″); and the Toquima Range (1750 km^2, 39°17′50″ to 38°29′9‴). Our data collection incorporated established techniques that detect species presence reliably and permit assessment of distributional trends (Pollard & Yates 1993; Pullin 1995; Bibby et al. 2000; Buckland et al. 2001; Siegel et al. 2001). These methods have been described in detail and tested for sampling adequacy (e.g., Fleishman et al. 1998, 2000, 2001; Mac Nally et al. 2004). Inventories for birds were conducted in 84 sites, and inventories for butterflies were conducted in 195 sites. Site areas ranged from 1.5 ha to 44.4 ha. The area of our study sites explained little variance in species richness (<3%) of either taxonomic group, perhaps because area often is not correlated with heterogeneity of topography or land cover in our study system, at least for locations smaller than mountain ranges (Mac Nally et al. 2003).

Model Building

We recorded 74 species of birds and 65 species of butterflies from our study sites (a complete list is available from E.F.). Site-level species richness ranged from 5 to 34 for birds (mean 17.3) and from 3 to 51 for butterflies (mean 24.9). We modeled the site-level species richness of birds (henceforth, bird species richness), butterflies (butterfly species richness), and both groups (combined species richness) as functions of the presence or absence of small subsets of "indicator" species. For each response variable (bird species richness, butterfly species richness, and combined species richness), we sought three sets of indicator species: birds only, butterflies only, or a combination of birds and butterflies. We limited the number of indicator species for each model to six, which is <10% of the number of species for each taxonomic group. We used Poisson regression to model species richness because Poisson error structures are appropriate for non-negative "counts" data such as number of species (McCullagh & Nelder 1989).

SELECTION OF INDICATOR SPECIES

With large sets of predictor variables, many of the screening approaches used to identify the "best" subset of variables are statistically suspect (Mac Nally 2000). Information criteria, such as Bayes information criterion (BIC; Schwarz 1978), have been recommended to identify the most efficient model(s) (Mac Nally 2000). The BIC enforces a compromise between model fit (ability to explain observed deviance in the response variable) and model complexity (number of predictor variables). The BIC is calculated as $-2 \times \log$ likelihood $+ \log(N) \times Q$, where N is the number of observations and Q is the number of model parameters. Ideally, all possible models are fitted, and the model with the lowest BIC value is retained.

Because we had such a large number of potential predictor variables (potential indicator species), it was impractical to fit all possible models, even if we considered only models with ≤ 6 predictors. We could have reduced the number of possible models by eliminating some species a priori on the basis of their distributions or other attributes (e.g., widespread, rare, or cryptic species; Mac Nally & Fleishman 2002). Only a severe pruning, however, which risks elimination of useful indicators, would have enabled us to fit all possible Poisson models. Another possibility would have been to conduct a less-severe pruning followed by an exhaustive search of ordinary multiple linear regression models, which can be computed more rapidly, but this process would not necessarily yield the best Poisson model per se. Instead, we employed a genetic algorithm to assess candidate Poisson models.

Genetic algorithms iteratively refine a "population" of potential solutions, usually generated randomly, by a process analogous to natural selection. The value of the function to be optimized—in our case, BIC for each model—is used as a measure of individual "fitness," with fitter individuals (models) given a greater probability of "reproducing." Genetic operations such as crossover and mutation are emulated and applied to a proportion of individuals in each generation. Therefore, characteristics of individuals with high fitness are retained and recombined until very good solutions are found.

We implemented a genetic algorithm by using the *R* statistical programming software (R Development Core Team 2003; Sekhon & Mebane 1998) to search for Poisson models with low BIC values for each of the nine combinations of response and predictor variables. First, an initial population of 1000 random models (individual "genomes") is generated. Each model in the population is encoded by a binary string of Q bits, where Q is the number of candidate predictors. Each bit corresponds to a potential predictor, which may be included in (1) or excluded from (0) the model. In the genetic analogy, the strings and bits are equivalent to chromosomes and individual genetic loci, respectively. In each generation, all models in the population are fitted as Poisson regression models with generalized linear modeling functions, and BIC is calculated for each model. Each model then is assigned a fitness rank according to its BIC value (fitness increases as BIC decreases). The model in each generation with the lowest BIC is propagated into the next generation. All other models are replaced with the results of genetic operators applied to parents selected, with replacement, from the entire population. The probability that a model will be selected as a parent decreases as its fitness decreases.

To produce offspring, five genetic operators are applied to selected parents in predetermined proportions: cloning (0.125), single-point mutation (0.375), multiple-point crossover (0.250), polytope crossover (0.125), and whole mutation (0.125). A clone is an exact replica of the parent model. Single-point mutation assigns a new value to one randomly selected bit (i.e., drops or adds one indicator species). Multiple-point crossover produces two offspring models from two parent models by exchanging randomly selected segments of strings between parents. Polytope crossover creates one offspring model that is a combination of as many parent models as there are bits (species). Whole mutation assigns a new, random value to all bits (i.e., randomly generates a new genotype). Because of the applied selective pressure, species (or "genes") present in models with low BIC (individuals with high fitness) are propagated throughout the population and, through crossover and mutations, are combined with new species until combinations with very high fitness are found. After 25 generations with no improvement in fitness (i.e., no reduction in the minimum BIC), the genetic algorithm terminates and the model with the lowest BIC (the solution) is reported.

Genetic algorithms can be trapped in local optima and, as with all heuristic methods, there is no guarantee that a particular solution is the best possible solution (global optimum). The concept of an absolute best regression model is vague in any case, and the model with the lowest BIC may not necessarily be the most useful model. Accordingly, we generated solutions from five random starts for each combination of response and predictor variables and then assessed the usefulness of each unique solution (from 1-5 solutions per combination, mean = 3.5) on the basis of model fit and attributes of indicator species (see Final Model Selection section).

In addition to searching for separate sets of indicator species for each response variable (bird species richness, butterfly species richness, and combined species richness), we searched for sets of "common" indicator species. To do this, we used the genetic algorithm to seek sets of ≤6 indicator species (from one or both taxonomic groups) that could be used to predict both bird species richness and butterfly species richness. We searched for three sets of common indicator species: birds only, butterflies only, and any combination of birds and butterflies. We modified the genetic algorithm to fit two models, one each with butterfly species richness and bird species richness as the response variable, for each individual in the population (i.e., for each unique set of indicator species). The BIC values were calculated for both models and summed for each individual. Fitness ranks then were assigned on the basis of summed BIC values.

MODEL FITTING

We computed parameters for each model selected by the genetic algorithm runs with the WinBUGS programming framework (Spiegelhalter et al. 2003). The model used was

$$\log(\mu_i) = \alpha_0 + \sum_{k=1}^{Q} \alpha_k X_{ik},$$
$$Y_i \sim \text{Poisson}\,(\mu_i),$$

where the αs are the regression coefficients to be estimated (an intercept [α_0] and coefficients for each of the Q indicator species); μ_i is the estimated mean species richness at site i given the presence or absence (X_i) of each of the Q indicator species; and Y_i is the observed species richness at site i, which is assumed to be distributed (~) as a Poisson variable with mean μ_i.

WinBUGS uses Markov chain Monte Carlo methods to iteratively estimate model parameters by repeatedly "sampling" from distributions specified in the model (Gilks et al. 1996). The Bayesian approach to estimating parameters formally incorporates prior knowledge about the value of a parameter and produces a posterior (or final) distribution of estimated values for each parameter. If one has virtually no prior knowledge about parameter values, it is appropriate to use a "noninformative" prior distribution for that parameter—typically a normal distribution with high variance—which means that the posterior probability distributions are dictated by the newly collected data (Lee 1989). We initially gave the αs noninformative normal priors [$\alpha \sim \text{normal}(\mu = 0, \sigma^2 = 1000)$]. Probability distributions for parameters were allowed to settle ("burn in") over 1000 iterations before posterior parameter distributions were built for another 3000 sampling iterations. Initial values were randomly generated.

We used the proportion of the posterior probability distributions of the estimated parameter values lying above or below zero (the posterior probability mass, PPM) to evaluate whether each indicator species contributed statistically to the prediction of species richness. We retained species if PPM $\geq$90%—that is, if at least 90% of the posterior probability distribution was either $>$0 (positive effect) or $<$0 (negative effect). Therefore, if PPM $<$90%, the corresponding species was omitted and the model was refitted. For a general overview of Bayesian statistical methods and associated terminology, see Bergerud and Reed (1998) and references therein.

FINAL MODEL SELECTION

Running the genetic algorithm and fitting models in WinBUGS generated from one to five candidate models for each response-predictor combination. Although the model with the lowest BIC is the best model found statistically (at least for the models searched), attributes of the indicator species also affect the usefulness of each model for predicting species richness. In particular, species that are difficult to detect or that have erratic patterns of occurrence among years may be unreliable indicator species even if their occupancy in at least 1 year is a good predictor of species richness. Thus, false negatives, or species recorded as absent from sites they do occupy in $\geq$1 year, decrease the accuracy of predictions of species richness. The probability of false negatives may be high for species that occupy sites infrequently even if surveys are repeated over several years and observer error is minimal (Mac Nally & Fleishman 2004). Therefore, we eliminated models containing indicator species with erratic occupancy patterns.

We used data from all sites that were surveyed for $\geq$2 years to calculate $p(- \mid \text{occupied})$, the probability of obtaining a false negative in a single year. This is the conditional probability that a species will be absent in any year from a site, given that it is known to occupy the site at some point in time. The probability of obtaining a false negative for surveys repeated over n years is $p(- \mid \text{occupied})^n$. To estimate this probability for each species, we used a Bayesian calculation to model the number of absences Y_i from occupied sites in n_i years as a Bernoulli trial with probability p_i, as follows:

$$\text{logit}(p_i) = \alpha,$$

$$Y_i \sim \text{binomial}(p_i, n_i),$$

$$p(-|\text{occupied}) = \frac{e^{\alpha}}{1 + e^{\alpha}},$$

where α is the log-odds ratio of $p(- \mid \text{occupied})$. We eliminated all models in which the maximum or mean values of $p(- \mid \text{occupied})$ for indicator species were $>$0.66 or $>$0.50, respectively. These values corresponded approximately to the tenth and fiftieth percentiles for $p(- \mid \text{occupied})$ for both birds and butterflies. We then selected the lowest BIC model for each response-predictor combination from the remaining models.

MODEL PREDICTIONS

We investigated the uncertainty of predictions of species richness made using each of the final models by applying those models to all possible combinations of indicator species presence and absence (i.e., to the 2^Q possible results of an inventory of Q indicator species at a site). We used WinBUGS to produce a posterior distribution of predicted richness values for each combination of indicators from which 95% credible intervals were calculated. Bayesian calculations produce probability distributions for model parameters, such as regression coefficients. One often uses "95% Bayesian credible intervals" (Lee 1989) to characterize the range of values for the parameter that encompasses 95% of the probability mass for that parameter. We calculated 95% credible intervals for a hypothetical, multiyear inventory in which the true occurrence of all indicator species is known (no false negatives).

Results

The genetic algorithm was an efficient method for identifying indicator species. All species selected as indicators contributed substantially (i.e., PPM > 90%) to predictions of species richness, demonstrating that the genetic algorithm identified indicator species with high explanatory capacity. Indicators in models for one taxonomic group always contributed to prediction of species richness of that group, and species selected as indicators in models for two taxonomic groups always contributed to the prediction of species richness for at least one of those groups.

We found promising models for all combinations of response variables (bird species richness, butterfly species richness, and combined species richness) and predictor variables (birds, butterflies, and both; Fig. 1) with selected models explaining 55–83% of deviances (mean = 74%; Table 1). After evaluating the false-negative probabilities of selected indicator species, we retained the lowest

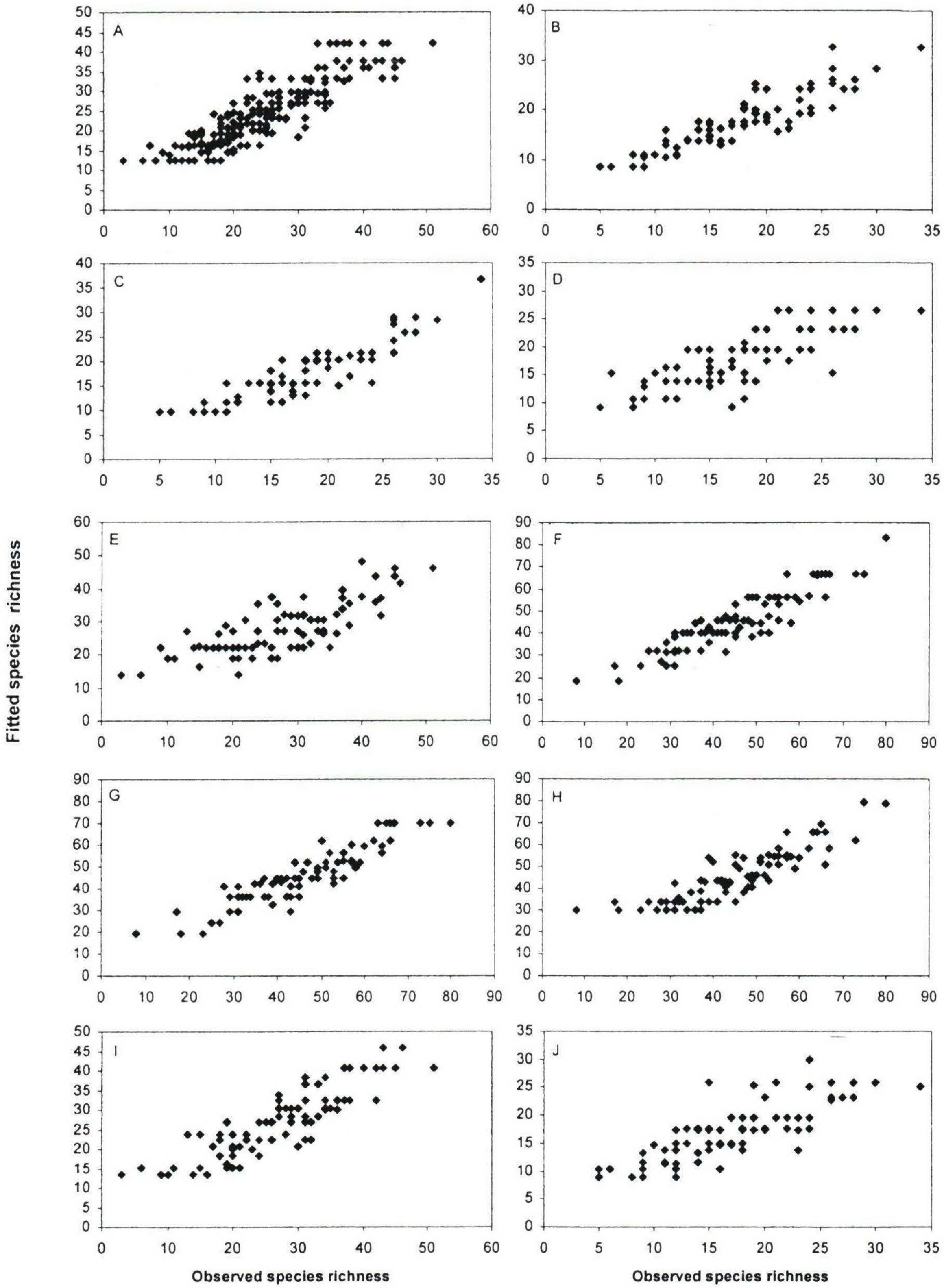

Figure 1. Fitted versus observed species richness for each combination of response variable and predictor variable: (a) butterfly species richness with butterfly indicators, (b) bird species richness with bird indicators, (c) bird species richness with combined indicators, (d) bird species richness with butterfly indicators, (e) butterfly species richness with bird indicators, (f) combined species richness with combined indicators, (g) combined species richness with butterfly indicators, (h) combined species richness with bird indicators, (i) butterfly species richness with combined "common" indicators, (j) bird species richness with combined common indicators.

Table 1. Parameter values (mean and standard deviation) for Poisson regression models of species richness of birds (bird S), butterflies (butterfly S), and both taxonomic groups (combined S) based on occurrence patterns of indicator species.

Variable (indicator species)	*Mean*	*Factor*[a]	*SD*	p(*occupied*)[b]	p(− | *occupied*)[c]
Butterfly S[d] with butterfly indicators					
(78% deviance explained, BIC[e] = 534)					
constant	2.519		0.051		
Icaricia lupini	0.266	1.30	0.037	0.69	0.44
Ochlodes sylvanoides	0.237	1.27	0.042	0.66	0.56
Papilio multicaudatus	0.203	1.23	0.035	0.51	0.47
Euchloe ausonides	0.162	1.18	0.031	0.50	0.49
Chlosyne acastus	0.113	1.12	0.031	0.49	0.27
Phyciodes mylitta	0.239	1.27	0.035	0.22	0.54
Bird S with bird indicators					
(82% deviance explained, BIC = 453)					
constant	2.150		0.072		
Black-throated Gray Warbler *(Dendroica nigrescens)*	0.222	1.25	0.067	0.68	0.23
MacGillivray's Warbler *(Oporornis tolmiei)*	0.234	1.26	0.067	0.58	0.17
Western Scrub-Jay *(Aphelocoma californica)*	0.251	1.29	0.062	0.54	0.49
Red-shafted Flicker *(Colaptes auratus)*	0.186	1.20	0.066	0.45	0.45
Western Tanager *(Piranga ludoviciana)*	0.140	1.15	0.060	0.38	0.47
Fox Sparrow *(Passerella iliaca)*	0.297	1.35	0.077	0.27	0.61
Bird S with combined indicators[f]					
(81% deviance explained, BIC = 451)					
constant	2.276		0.068		
Western Scrub-Jay *(Aphelocoma californica)*	0.289	1.33	0.059	0.54	0.49
Audubon's Warbler *(Dendroica coronata)*	0.263	1.30	0.058	0.38	0.47
Fox Sparrow *(Passerella iliaca)*	0.350	1.42	0.065	0.27	0.61
Incisalia eryphon	0.185	1.20	0.071	0.64	0.31
Satyrium sylvinum	0.240	1.27	0.070	0.13	0.44
Bird S with butterfly indicators					
(63% deviance explained, BIC = 479)					
constant	2.375		0.075		
Incisalia eryphon	0.417	1.52	0.068	0.64	0.31
Pontia beckerii	−0.167	0.85	0.064	0.55	0.33
Papilio multicaudatus	0.345	1.41	0.062	0.51	0.47
Speyeria nokomis	0.307	1.36	0.079	0.07	0.50
Butterfly S with bird indicators					
(55% deviance explained, BIC = 599)					
constant	2.946		0.046		
Rock Wren *(Salpinctes obsoletus)*	0.156	1.17	0.043	0.56	0.39
Western Tanager *(Piranga ludoviciana)*	0.203	1.22	0.043	0.38	0.47
Yellow Warbler *(Dendroica petechia)*	0.315	1.37	0.044	0.35	0.35
Black-headed Grosbeak *(Pheucticus ludovicianus)*	0.151	1.16	0.048	0.33	0.55
Chukar *(Alectoris chukar)*	0.259	1.30	0.063	0.13	0.41
Western Meadowlark *(Sturnella neglecta)*	−0.310	0.73	0.080	0.10	0.37
Combined S with combined indicators					
(83% deviance explained, BIC = 565)					
constant	2.902		0.097		
Yellow-breasted Chat *(Icteria virens)*	0.216	1.24	0.074	0.04	0.64
Hesperia comma	0.336	1.40	0.090	0.92	0.11
Incisalia eryphon	0.233	1.26	0.039	0.64	0.31
Papilio multicaudatus	0.346	1.41	0.035	0.51	0.47
Satyrium behrii	0.213	1.24	0.036	0.50	0.41
Polygonia zephyrus	0.172	1.19	0.036	0.32	0.65
Combined S with butterfly indicators					
(82% deviance explained, BIC = 568)					
constant	2.957		0.094		
Hesperia juba	0.410	1.51	0.095	0.87	0.18
Incisalia eryphon	0.217	1.24	0.041	0.64	0.31
Papilio multicaudatus	0.217	1.24	0.044	0.51	0.47
Nymphalis antiopa	0.156	1.17	0.042	0.50	0.50
Polygonia zephyrus	0.130	1.14	0.038	0.32	0.65
Phyciodes mylitta	0.165	1.18	0.044	0.22	0.54

continued

Table 1. (continued)

Variable (indicator species)	*Mean*	*Factor*[a]	*SD*	p(*occupied*)[b]	p(− | *occupied*)[c]
Combined S with bird indicators					
(72% deviance explained, BIC = 604)					
constant	3.393		0.036		
Rock Wren *(Salpinctes obsoletus)*	0.126	1.13	0.036	0.56	0.39
Western Tanager *(Piranga ludoviciana)*	0.239	1.27	0.033	0.38	0.47
Yellow Warbler *(Dendroica petechia)*	0.254	1.29	0.037	0.35	0.35
Black-headed Grosbeak *(Pheucticus ludovicianus)*	0.176	1.19	0.035	0.33	0.55
Song Sparrow *(Melospiza melodia)*	0.175	1.19	0.040	0.29	0.33
Red-tailed Hawk *(Buteo jamaicensis)*	0.247	1.28	0.065	0.06	0.61
Butterfly S with "common" indicators[g]					
(73% deviance explained, BIC = 540)					
constant	2.605		0.070		
Gray Flycatcher *(Empidonax wrightii)*	0.121	1.13	0.049	0.43	0.46
Warbling Vireo *(Vireo gilvus)*	0.182	1.20	0.051	0.39	0.09
Ochlodes sylvanoides	0.385	1.47	0.068	0.66	0.46
Satyrium behrii	0.302	1.35	0.047	0.50	0.41
Lycaena rubidus	0.231	1.26	0.047	0.19	0.57
Bird S with "common" indicators					
(68% deviance explained, BIC = 479)					
constant	2.173		0.085		
Mountain Chickadee *(Poecile gambeli)*	0.279	1.32	0.055	0.58	0.31
Gray Flycatcher *(Empidonax wrightii)*	0.247	1.28	0.064	0.43	0.46
Warbling Vireo *(Vireo gilvus)*	0.533	1.70	0.066	0.39	0.09
Ochlodes sylvanoides	0.161	1.17	0.075	0.66	0.46
Lycaena rubidus	0.108	1.11	0.061	0.19	0.57

[a] *A multiplicative factor (the exponentiated mean,* e^{mean}*) by which the presence of the indicator species affects the predicted species richness.*
[b] *Probability that a site is ever occupied by that species (i.e., the proportion of sites occupied).*
[c] *Conditional probability that a species will be absent in any year from a site given that it is known to occupy the site at some point in time.*
[d] *Species richness.*
[e] *Bayes information criterion.*
[f] *Combined indicators include both birds and butterflies.*
[g] *A single set of species that can be used to predict species richness of both birds and butterflies.*

BIC models for all but two response-predictor combinations. The lowest BIC models predicting butterfly species richness and combined species richness with butterfly indicators both included one species with a false negative probability that we deemed unacceptably high, *Colias philodice* [$p(- \mid \text{occupied}) = 0.77$]. As a result, we rejected the latter models in favor of the models with second-lowest BIC values. In both cases, the retained model included many of the same indicator species as the rejected model (three for combined species richness and four for butterfly species richness) and had similar fit (within 2% explained deviance).

Model predictions with 95% credible intervals are shown in Fig. 2. Credible intervals were relatively narrow but widened with increasing predicted species richness because the response variables had Poisson distributions (i.e., mean equal to variance).

Species Richness of One Taxonomic Group

The best-fitting models of bird species richness and butterfly species richness included only indicator species from the same taxonomic group as the response variable. The best models of bird species richness with birds as indicators and butterfly species richness with butterflies as indicators each included six indicator species and explained 82% and 78% of deviances, respectively (Table 1). Sample sizes for models of butterfly species richness (195 sites) were much larger than those for models of bird species richness (84 sites).

Using species from both taxonomic groups as potential predictors did not improve explanatory capacity for butterfly species richness. Genetic algorithm solutions did not include bird species as predictors of butterfly species richness if butterflies were also available as predictors. Only the 84 sites surveyed for birds as well as butterflies could be included in searches for models using both taxonomic groups as predictors. As a result, the predictors and fit of the best model of butterfly species richness with combined indicators, which included only butterflies as predictors, were not identical to those of the best model of butterfly species richness with butterflies as indicators (data from 195 sites). The two models did, however, have three indicator species in common (*Icaricia lupini, Ochlodes sylvanoides,* and *Chlosyne acastus*). We present only the latter model because it includes all available data and is likely to be the most useful (Table 1).

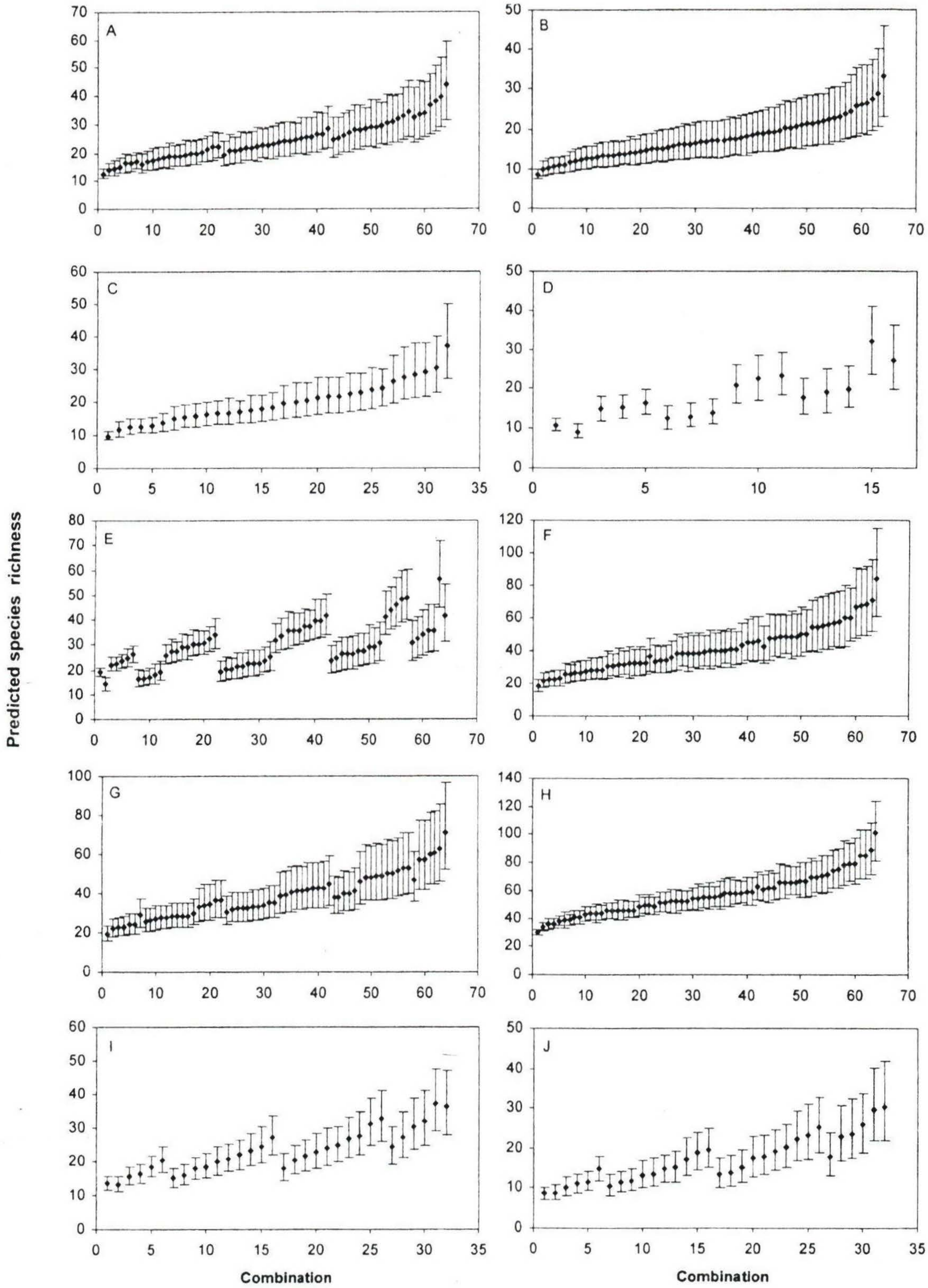

Figure 2. Predicted species richness values and 95% credible intervals versus each possible combination of indicator species presence and absence: (a) butterfly species richness with butterfly indicators, (b) bird species richness with bird indicators, (c) bird species richness with combined indicators, (d) bird species richness with butterfly indicators, (e) butterfly species richness with bird indicators, (f) combined species richness with combined indicators, (g) combined species richness with butterfly indicators, (h) combined species richness with bird indicators, (i) butterfly species richness with combined "common" indicators, (j) bird species richness with combined common indicators.

Using both taxonomic groups as predictors of bird species richness resulted in a slight improvement in model parsimony. The fit of a model including three bird species (two of which were included in the model of bird species richness with birds as indicators) and two butterfly species as predictors (81% deviance explained) was similar to a six-species model of bird species richness with birds as indicators (82% deviance explained; Table 1).

Models of species richness of one taxonomic group based on indicator species drawn exclusively from a different taxonomic group had poorer fits than within-taxon models or combined models; nonetheless, we identified potentially useful indicators. A model with just 4 butterfly indicator species explained 63% of the deviance in bird species richness (Table 1). This model was the only solution produced by five runs of the genetic algorithm, suggesting that these 4 butterfly species were substantially better predictors of bird species richness than were other butterfly species. The latter inference was supported by the results of an additional genetic algorithm run that was constrained to optimize, with ≤ 6 indicator species, model fit (percent deviance explained) rather than BIC. The best solution added 2 species to the existing model but had only marginally better fit (66% deviance explained).

The best model of butterfly species richness with birds as indicators explained 55% of deviance and included 6 indicator species (Table 1). One of these species, Western Meadowlark (*Sturnella neglecta*), had a negative coefficient, indicating a negative association with butterfly species richness. Prediction of butterfly species richness with bird indicator species could be improved by including ≥ 6 indicator species in the model. For example, models with 7 bird indicator species explained $>60\%$ of deviance in butterfly species richness.

Species Richness of Two Taxonomic Groups

Butterfly species were better indicators of combined species richness than were bird species (Table 1). The best model of combined species richness included five butterfly species and one bird species and explained only 1% more deviance (83%) than a model with six butterfly species (82%). Nonetheless, bird species alone could be used to predict combined species richness, with a six-species model explaining 72% of deviance.

Our search for a common set of species that could be used to predict both bird and butterfly species richness yielded promising results. We built models explaining 68% and 73% of species richness of birds and butterflies, respectively, with a common set of three bird species and three butterfly species. Four of these species (two birds, Gray Flycatcher [*Empidonax wrightii*] and Warbling Vireo [*Vireo gilvus*], and two butterflies, *Ochlodes sylvanoides* and *Lycaena rubidus*) were included in both models, whereas the remaining bird (Mountain Chickadee [*Poecile gambeli*]) and butterfly (*Satyrium behrii*) were retained only in models predicting richness of their own taxonomic group.

We also identified a set of six species of butterflies that might reasonably predict both bird species richness and butterfly species richness. This set included the four indicator species in the best model of bird species richness and two additional species, *Ochlodes sylvanoides* and *Lycaena heteronea*. These six species explained 70% of the deviance in butterfly species richness. The additional two species did not improve the fit of the model of bird species richness. Thus, a set of six butterfly indicator species yielded good models of both bird species richness (four indicator species, 66% of deviance explained) and butterfly species richness (six indicator species, 70% of deviance explained).

The best set of six common bird indicator species explained 66% of deviance in bird species richness and 48% of deviance in butterfly species richness. It probably would be necessary to increase the total number of bird indicator species to adequately predict both bird species richness and butterfly species richness. Three of the six bird species identified as indicators of butterfly species richness, Western Tanager (*Piranga ludoviciana*), Yellow Warbler (*Dendroica petechia*), and Black-headed Grosbeak (*Pheucticus ludovicianus*), also had capacity to predict bird species richness (a model including only the latter three species explained 54% of deviance of bird species richness). Western Tanager, Yellow Warbler, and Black-headed Grosbeak could be combined with three additional species, Western Scrub-Jay (*Aphelocoma californica*), Red-shafted Flicker (*Colaptes auratus*), and Song Sparrow (*Melospiza melodia*), to produce a model that explained 77% of deviance of bird species richness. Thus, a set of nine bird indicator species yielded a good model of bird species richness (six indicator species, 77% of deviance explained) and a reasonable model of butterfly species richness (six indicator species, 55% of deviance explained).

Discussion

Our work suggests that although indicator species probably are most effective within taxonomic groups, it is possible to identify suites of species whose occurrence patterns explain high percentages of deviance—sometimes more than 80%—in species richness of multiple taxonomic groups. Occurrence of species in one taxonomic group could be used to explain species richness of a different taxonomic group, and species richness of two taxonomic groups could be explained using species drawn from either one or both of those groups. Moreover, our work demonstrated that a common set of species can provide information on the species richness of two taxonomic groups, implying that it may be possible to use relatively few indicator species to predict separately the species richness of multiple taxonomic groups. Our modeling framework is applicable to any ecosystem and may be a useful tool for estimating cross-taxonomic species richness at scales pertinent to conservation and land management. Whether a given threshold of explanatory or predictive accuracy (e.g., 80%) is "good enough" is inevitably context specific. Each real-world situation must be considered to determine the optimum trade-off between the ability and need to make predictions and the accuracy of those predictions.

The genetic algorithm, an iterative screening approach that emulates the process of natural selection, appeared to be an excellent method for rapidly identifying useful combinations of predictor species from astronomically large numbers of possible combinations, reducing the need to use inappropriate model error structures or to fit all possible models. Exhaustive model searches will be impossible for many systems, especially when multiple taxonomic groups are considered. Genetic algorithms can be used to identify indicator species from any system. Indeed, genetic algorithms may prove useful in any modeling task that requires identification of a suitable subset of a large number of potential predictor variables.

A model that explains considerable deviance in the data used for its creation should not be used to guide conservation and land management unless it also makes effective predictions. Thus, prediction of species richness based on any functional relationship, including occurrence of indicator species, should be regarded as a testable hypothesis to be confronted with newly collected test data (Landres et al. 1998; Mac Nally et al. 2000; Fleishman et al. 2003; Mac Nally & Fleishman 2004). Based on much experience with real data sets, we believe cross-validation is inadequate for evaluating the utility of predictive models. Accordingly, we are in the process of collecting validation data to facilitate tests of the models presented here. In terms of both biogeography and land use, mountain ranges are an appropriate scale for developing and testing the transferability (sensu Leftwich et al. 1997) of indicator species models in this geographic region. If the models successfully predict species richness, we will combine the model building and validation data sets to yield an improved or "updated" model that more effectively represents species richness patterns over a large area (Hilborn & Mangel 1997; Mac Nally & Fleishman 2004). Previous work on prediction of butterfly species richness with butterfly indicators gives us much cause for optimism about the success of the current models (Mac Nally & Fleishman 2004).

Species Richness of One Taxonomic Group

Models of species richness of single taxonomic groups based on same-taxon indicator species explained approximately 80% deviance and did not appear to be highly sensitive to number of locations used to build the model. Regardless of response-predictor combination, effective indicator species collectively represented the variety of land-cover associations in the taxonomic group(s) for which they conveyed information about species richness. For example, the model of bird species richness with birds as predictors included two species, each associated with relatively dry vegetation (Western Scrub-Jay, Black-throated Gray Warbler [*Dendroica nigrescens*]), riparian vegetation (MacGillivray's Warbler [*Oporornis tolmiei*], Fox Sparrow [*Passerella iliaca*]), and mixed vegetation (Red-shafted Flicker, Western Tanager). Similarly, the model of species richness of butterflies with butterflies as predictors included species whose larvae feed on a full range of vegetation growth forms (Fleishman et al. 1997): grasses (fed on by *Ochlodes sylvanoides*), forbs (*Icaricia lupini, Chlosyne acastus, Phyciodes mylitta*), shrubs (*Euchloe ausonides*), and trees (*Papilio multicaudatus*). Moreover, each of the latter six butterfly species uses at least two of the three most prominent local topographic features (dry canyons, riparian canyons, and uplands), and the six species represent all five families of butterflies present in the Great Basin.

The fit of models of species richness for one taxonomic group was not improved by including indicator species from a second taxonomic group. Models of butterfly species richness, in particular, were not improved by including birds. A potential explanation may be that in the Great Basin, most if not all land-cover types used by birds are also used by butterflies. Butterflies, however, are typically diverse and abundant in meadows, a land-cover type that provides relatively few resources for birds, especially when subject to livestock grazing and recreational use (Warkentin & Reed 1999). Differences in occurrence patterns of birds and butterflies with respect to land cover may explain why genetic algorithm solutions did not include birds as predictors of butterfly species richness if butterflies were also available as predictors and why butterflies were better indicators of combined species richness than birds. Consistent with this hypothesis, the model of bird species richness with butterflies as indicators included one species primarily associated with low-elevation grasses and shrubs, *Pontia beckerii*. Sites at which *P. beckerii* was present usually had lower bird species richness than sites at which it was absent.

There was a slight improvement in model parsimony (i.e., fewer indicator species could be used to explain a similar percentage of deviance) when indicator species from two taxonomic groups were used to predict bird species richness. In practice, the advantages of surveying or monitoring indicator species from a single taxonomic group likely would outweigh the benefit of including one fewer indicator species in a model of species richness.

Practical Applications of Predictions for Multiple Taxonomic Groups

Our results suggest that information from different taxonomic groups can be pooled to predict species richness of a comprehensive biota. Among the most promising outcomes of our work is the discovery that it may be possible to use a common set of species to predict species richness for more than one taxonomic group. For example, 68% of bird species richness and 73% of butterfly species richness could be explained using a set of three species of birds and three species of butterflies, four of which were included in both models. If sufficient data existed, our methods certainly could be applied to a larger number of taxonomic groups in an effort to identify reliable indicators of species richness for a comprehensive set of plants and animals in a given ecosystem or geographic region. Alternatively, it may be more effective to use our methods to select, in turn, indicators within each taxonomic group of conservation concern.

Given that rare species often do not occur in locations with greatest species richness, it may not be possible to draw inferences about the presence of rare species on the basis of indicators of species richness with any method (Lawler et al. 2003). None of the birds or butterflies in our study system is listed as threatened or endangered, and there are no species-level endemics. Also, definition and estimation of rarity in the context of large-scale land management presents substantial challenges. In our study system, occurrence rates of individual species often vary among mountain ranges (Fleishman et al. 2003). Moreover, low occurrence rates may not equate to extinction risk: the relatively uncommon resources used by some species of birds and butterflies with low rates of occurrence, such as plants with patchy distributions, are not directly threatened by current land uses.

Efforts to identify surrogate-based approaches to estimate species richness and other measures of ecological status are popular because inventory data for many regions are insufficient to directly inform conservation and land-use planning decisions. Accordingly, a method for selecting indicator species that requires relatively complete species data might appear to be anything but a shortcut. Our methods, however, select indicator species potentially applicable across an extensive landscape on the basis of data that, although representative of the larger system, are collected from a small fraction of the total land area. Across planning landscapes of tens to hundreds of thousands of square kilometers, we believe the method is a realistic approach to deriving estimates of species richness that can inform strategies for allocation of multiple land uses, including conservation. The Great Basin, for example, covers more than 400,000 km^2 and includes pproximately 350 major mountain ranges. If indicator pecies identified on the basis of data collected from sections of three mountain ranges can be used to predict species richness at any location even within the 30,000 km^2 biogeographic subregion in which our work was centered (Austin & Murphy 1987), we believe that the method can serve as an effective and practical tool for prioritizing management activities.

Comparative values of species richness are used as a primary criterion for establishing conservation and management priorities. The lack of data, money, and time has prompted scientists and practitioners to seek shortcuts for estimating species richness. Our work is the first to demonstrate empirically not only that species richness of one taxonomic group can be explained using indicators drawn from the same taxonomic group, but also that individual and combined species richness of two taxonomic groups can be explained using indicator species drawn either from both of those groups or exclusively from one of the groups. Our approach to selecting indicator species may help provide reliable data on species richness for meeting biological objectives in diverse assemblages and ecosystems. In addition, by developing and testing hypotheses to explain why particular species convey information about a larger biota, we gain insight into patterns and drivers of species richness and the nature of ecological assemblages.

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